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Paleoneurological Studies in Honor of Ralph L. Holloway  
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NUMBER 4

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# THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies  
in Honor of Ralph L. Holloway



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FRONT COVER CAPTIONS

*Center: Portrait of Ralph L. Holloway.*

*Upper left: A modern human brain.*

*Upper right: Ralph measuring landmarks on an endocast ca. 1976.*

*Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).*

*Lower left: Ralph with an endocast of the Flores "hobbit" cranium.*

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# CHAPTER 7

## CEREBELLUM AND BRAIN EVOLUTION IN HOLOCENE HUMANS

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ANNE H. WEAVER

### ABSTRACT

Evolutionary development of the cerebellum and its implications for human cognitive evolution must be considered in the broader framework of hominin brain evolution—a gradual, complex process that involved heterochrony in response to genetic evolution, cultural innovation, population dynamics, and environmental challenges over an extended time. This chapter offers a chronology of relevant events and a proposed scenario that integrates the presently available data relating to cerebellar evolution in Late Pleistocene and Holocene humans (150,000 years BP to the present.)

### INTRODUCTION

Overall brain volume in the genus *Homo* reached its maximum by the late Middle Pleistocene (>150,000 years BP), and then declined somewhat thereafter, probably in response to a decrease in body mass (Ruff, Trinkaus et al., 1997).

The relative proportions of the cerebellum and cerebral hemispheres continued to change as well, suggesting that cerebellar-neocortical interactions remained under selection. In recent humans, the cerebral hemispheres are relatively smaller and the cerebellum relatively larger than in terminal Pleistocene humans. The cerebellum did not reach modern proportions until the very late Pleistocene (some time after 28,000 years BP) postdating by several thousand years the appearance of modern humans in territories occupied by archaic human groups (Weaver, 2001; Weaver, 2005).

This pattern of continued cerebellar evolution is consistent with fossil, archeological and genetic evi-

dence that human behavior and morphology, including brain morphology, have continued to evolve since the Late Pleistocene (Hawks, Wang et al., 2007).

Temporal correlations between divergent lines of evidence can stimulate causal hypotheses about the genetic and cultural dynamics that interacted to produce brain morphology and related cognitive patterns characteristic of living humans. The purpose of this paper is to outline chronological developments that may have contributed to cerebellar evolution, summarize the present state of the evidence, and suggest further directions for research.

### CHRONOLOGY FOR ARCHAIC AND MODERN HUMAN POPULATIONS

Dating of fossil and archeological remains during the crucial Late Pleistocene period has been subject to a flurry of recent revisions related to refined methodologies in analysis and calibration of Carbon-14 ( $^{14}\text{C}$ ) dates. The chronology outlined below will rely on uncalibrated dates because they are the most accessible and consistent. However, the reader should note that uncalibrated dates tend to underestimate calendar years. For current discussions of the implications of reanalysis and redating of critical fossils and sites, refer to Trinkaus (Trinkaus, 2005), Mellars (Mellars, 2006), and Zilhão (Zilhão, 2006).

By the end of the Middle Pleistocene (250,000 years BP), Africa and Eurasia were populated by scattered groups of fairly large-brained, sturdy-bodied humans known as “early archaic *Homo sapiens*.” They were descendants of *Homo erectus*, who had spread from Africa over the preceding 1.5 million years. Early archaic

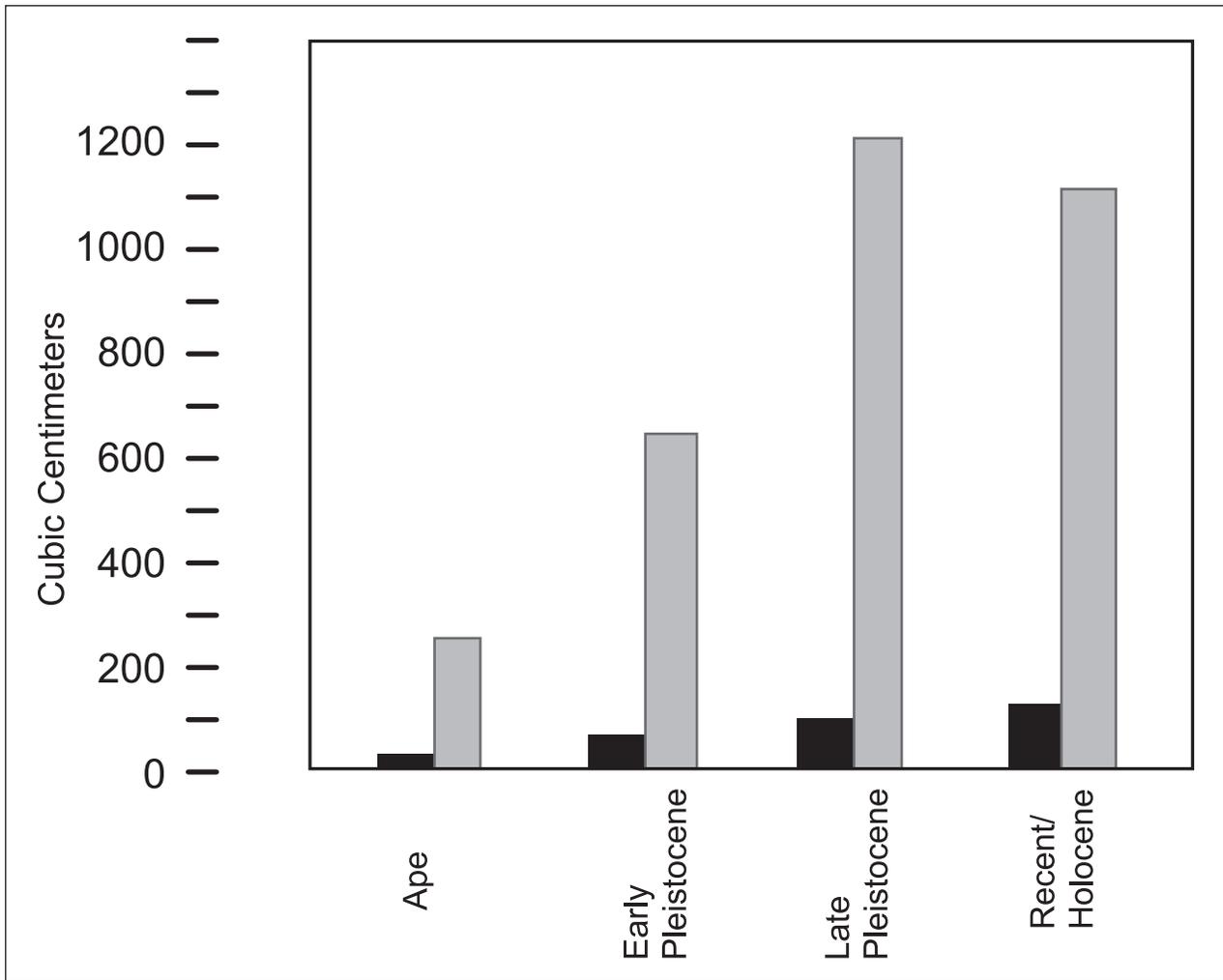


Figure. 1. Stages in cerebellar evolution. Light Gray = cerebral hemisphere volume; Dark Gray = cerebellum volume. Early–Middle Pleistocene includes *Homo habilis*, *Homo erectus*, and early archaic *Homo sapiens*. Late Pleistocene includes Neandertals and *Cro-Magnon 1*.

*Homo sapiens* gave rise to two populations of particular interest: Neandertals and anatomically modern humans.

Neandertals are a regional variant of late archaic *Homo sapiens* who inhabited Europe and Western Asia. Neandertals are distinguished from other late archaic *Homo sapiens* by their “cold adapted” body proportions, expanded nasal morphology, and other dental, skeletal and craniofacial features (Trinkaus, 2006). Individual distinctive Neandertal features are present in European fossils as old as 400-600,000 years BP (Bischoff, Shamp et al. 2003) but the “classic” Neandertal pattern did not coalesce until after 75,000 years BP. The most recent reliably dated diagnostic Neandertal remains have been radiocarbon dated to 32-33,000 years BP (Higham, Ramsey et al., 2006).

In Africa, archaic *Homo sapiens* gave rise to another distinct lineage, destined to become the ancestors of recent humans, approximately 200,000 years BP. Like Neandertals, they were large-brained. These hominins were characterized by their shorter faces, smaller incisors, narrower noses, and prominent chins, along with derived postcranial features especially notable in the shoulder

and pelvis (Trinkaus, 2006). Because Holocene humans share these characteristics, this group of fossils and later ones that resemble them are known as “early anatomically modern *Homo sapiens*.” They are considered to be the direct ancestors of contemporary humans. Anatomically modern humans were apparently confined to Africa until 50,000-60,000 years BP, (with brief incursions into the Levant ca. 90,000 years BP) (Vandermeersch, 1981; Tillier, 1999).

Anatomically modern humans reached Australia by 50,000 years BP (Brown, 1992), Eastern Asia by 30,000 years BP (Trinkaus, 2005), and the Americas by at least 12,500 years BP (Dillehay, 1999).

The pattern of interaction between anatomically modern humans and the archaic populations they encountered as they spread out of Africa is ambiguous. A thorough analysis of the archeological, skeletal and genetic evidence precludes contact between anatomically modern humans and Neandertals prior to 43,000 years ago. Then, within a brief period of about 1,000 years, admixture, competition and conflict had resolved the distinctive modern and human population differences be-

tween the two groups. Neandertal skeletal features persisted in scattered hybrid descendants (Trinkaus 2006), but gradually decreased in frequency until few overt traces remained. To date, analyses of Neandertal DNA suggest that they may have made a minimal, as yet poorly defined, contribution to the modern human gene pool, perhaps through limited interbreeding between modern males and Neandertal females (Trinkaus, Moldovan et al., 2003; Green, Krause et al., 2006; Noonan, Coop et al., 2006; Zilhão, 2006). A recent study has identified *microcephalin* variant *MCPHI*, which appears to affect neocortical and cerebellar development (Trimborn, Bell et al., 2004), as an introgressive gene from late archaic humans—possibly Neandertals. (See discussion below.) (Evans, Mekel-Bobrov et al., 2006; Zilhão, 2006).

## ENDOCRANIAL MEASUREMENTS IN FOSSILS

Brain size in fossils is estimated from endocranial capacity. Relative brain size in fossil hominins is customarily expressed as an encephalization quotient, or “EQ,” (Jerison, 1974) which represents logged values for actual/expected brain size for a given body mass. The best estimates of body mass and endocranial volumes for Late Pleistocene archaic and modern humans suggest that, despite their absolutely larger brains, mean EQ in Neandertals was slightly lower than that of anatomically modern humans, although there is considerable overlap at the lower end of the modern human range of variation (Ruff, Trinkaus et al., 1997; Rosenberg, Zune et al., 2006).

Neandertals, like other archaic humans, have elongated braincases, with low, sloping foreheads. However, their frontal lobe profiles, recorded on the inner table of the skull, do not differ significantly from modern humans (Bookstein, Schäfer et al., 1999; Holloway, Broadfield et al., 2004). Asymmetry of the cerebral hemispheres, well established in hominins since the early Pleistocene (Begun and Walker, 1993), is similar in Neandertals and anatomically modern humans, suggesting a similar pattern of functional lateralization. On the basis of differences in parietal proportions (at least with regard to chord measurements), have led Bruner (Bruner, 2004) to suggest that brain expansion in Neandertals and early modern humans may have followed independent evolutionary trajectories. However, as described below, the archeological record indicates that both groups engaged in similar subsistence behaviors and developed similar technical expertise over time (Mellars, 2006; Zilhão, 2006; Zilhão, d’Errico et al., 2006).

## RELATIVE CEREBELLAR VOLUME

Cerebellum size in fossil hominins can be estimated from the volume of the posterior cranial fossa, which is highly correlated with cerebellum volume (Weaver, 2005). To date, cerebellar volume estimates for fossils

are available for a total of 18 fossil hominins. The Late Pleistocene sample includes one anatomically modern human (Cro-Magnon I; 28,000 years BP); and three classic Neandertals (La Chapelle I, La Ferrassie I, and Gibraltar/Forbes Quarry (Weaver, 2005). The recent human comparative sample incorporates data for over 1,450 individuals, collected from multiple sources (Weaver, 2005). Such a large data set for modern humans permits a degree of statistical robusticity, despite the small size of the fossil sample. Nonetheless, it should be emphasized that the present fossil sample is very small and interpretations based on such a limited sample are tentative.

The data indicate that recent humans have cerebella that are both absolutely and relatively larger than *any* of the Late Pleistocene humans. As a consequence, *the cerebral hemispheres of contemporary humans are proportionately smaller than they are in Neandertals and Cro-Magnon 1* (Weaver, 2005).

The brain is a costly organ to maintain, despite its putative contribution to evolutionary fitness. It is likely that increased cerebellar volume represents a fitness advantage to Holocene and recent humans, reflected in a more useful or efficient cognitive strategy without an increase in overall brain mass.

## EVOLUTION IN GENES THAT CONTRIBUTE TO BRAIN DEVELOPMENT

Continued cerebellar evolution coincides with changes in relative frequency of a number of genes involved in regulating brain development. These genes appear to have been subject to positive Darwinian selection. Notable among them are *microcephalin*, *ASPM*, and *FOXP2* (Vargha-Khadem, Watkins et al., 1995; Vargha-Khadem, Watkins et al., 1998; Lai, Fisher et al., 2001; Enard, Przeworski et al., 2002; Evans, Anderson et al., 2004; Evans, Anderson et al., 2004; Shu, Cho et al., 2005; Evans, Mekel-Bobrov et al., 2006; Evans, Vallender et al., 2006). At present, the confidence intervals related to the timing of mutations in these genes are very broad. In addition, functional contributions of these genes to brain morphology and their possible contributions to cognitive behavior are poorly understood. However, temporal correlations between changes in these genes brain and behavioral changes are suggestive.

*Microcephalin* is of particular interest, because one variant (*MCPHI*) may have passed from Neandertals or other archaic humans into the anatomically modern gene pool (Evans, Anderson et al., 2004; Evans, Mekel-Bobrov et al., 2006). *Microcephalin* plays a critical role in brain size regulation. It appears to affect cerebellar size as well (Trimborn, Bell et al., 2004). Its influence on the cerebellum may be the result of a global developmental effect that manifests during the proliferation phase of neurogenesis. Analysis of the *MCPHI* allele suggests that it entered the gene pool of anatomically modern humans at or sometime before 37,000 ( $\pm 23,000$ ) years BP from an archaic human population. As a result of posi-

tive selection, this allele has now reached a frequency of 70% in recent humans. The very high frequencies of this allele in eastern Siberia (98%) and in indigenous American populations (92-100%) seem to indicate that this allele was well established prior to the entry of humans into the Americas.

Unfortunately, both genetic and quantitative morphological data for Australian brain morphology are severely lacking. There is some evidence that cerebellar proportions in indigenous Australians are atypical. (Klekamp, Riedel et al., 1987; Klekamp, Riedel et al. 1989) Additional genetic and volumetric data for Australian populations could be highly informative in determining which alleles, if any, may have entered the modern human gene pool subsequent to human dispersal into Australia.

*ASPM*, another allele that is expressed in the cerebellum and also contributes to brain size may have affected brain evolution in hominins. *ASPM* appears to have been subject to positive selective pressure after the split of humans and chimpanzees (5-7 million years BP) but before modern humans left Africa (Zhang, 2003; Evans, Anderson et al., 2004). One variant of *ASPM*, haplotype 63, appeared ~5800 years BP (95% confidence interval 14,100 - 500 years), and may be subject to ongoing positive selection (Mekel-Bobrov, Gilbert et al., 2005).

Neither *microcephalin MCPH1* nor *ASPM* haplotype 63 has reached fixation in the human genome as a whole. Their present-day differential distribution across global populations may reflect alternate but equivalent cognitive strategies in living humans; mutations that were subject to positive selection in the past; or atypical historical population dynamics.

The *FOXP2* gene has received considerable attention due to its apparent role in regulating social communication in many organisms. Disruption of this gene in humans manifests in problems with grammar and speech production, non-verbal intelligence, and non-speech related movements of the mouth and face. *FOXP2*, a transcription factor, appears to affect development of several brain regions, most notably the caudate nucleus of the basal ganglia (Vargha-Khadem, Watkins et al., 1995; Vargha-Khadem, Watkins et al., 1998; Lai, Fisher et al., 2001; Shu, Cho et al., 2005). Experiments with mice suggest that *FOXP2* is involved in regulating cerebellar development and neural migration as well (Shu, Cho et al., 2005; Brumwell and Curran, 2006). This gene has apparently come under selection in recent human evolution, undergoing a selective sweep between 100,000 years and 10,000 years BP (Enard, Przeworski et al., 2002). *FOXP2* may indeed play a role in human cognitive evolution. However, it is important to emphasize that no single gene can possibly account for the emergence of the complex, highly distributed, redundant, and flexible set of cognitive behaviors involved in human language.

## CEREBELLAR EVOLUTION & COGNITION

Many researchers have suggested that the specialized architecture of the cerebellum enables it to process neural data regardless of whether they arise in “sensory”, “motor”, or “association” areas of the neocortex (Leiner, Leiner et al., 1986; Ito, 1993; Houk and Wise, 1995; Ariada-Mendicoa, Otero-Silceo et al., 1999; Fox, Sitompul et al., 1999; Houk and Miller, 2001; Middleton and Strick, 2001; Houk, 2005). There is a growing consensus that the cerebellum makes a significant contribution to higher cognitive functions, including planning of future actions, working memory, visual perception, directed attention, and rule-based learning.

The archeological record supports the hypothesis that intensified demands related to these quintessentially human cognitive behaviors coincided with cerebellar evolution. Schoenemann (Schoenemann, 2006) summarizes social and ecological factors that may have intensified selective pressures for brain evolution during the course of hominid evolution. Following is a brief chronology focusing on behaviors that emerged as part of the archeological record of the Holocene, in comparison to those already in place by the Late Pleistocene. Again, however, it must be noted that temporal correlations are not causally definitive. While the data are thought-provoking, they are not conclusive.

By the Late Pleistocene, and prior to cerebellar expansion, both late archaic and anatomically modern humans had mastered a complex repertory of culturally-based subsistence techniques related to complex foraging, invented and maintained for thousands of years by large-brained hominins. For example, more than 80,000 years ago Neandertals had mastered a tightly-controlled and complex series of processes, including the advanced pyrotechnology, needed to manufacture adhesive pitch from birch bark. A fingerprint and wood fragments indicate that the pitch was used to fashion hafted tools (Koller, Baumer et al., 2001; Zilhão, 2006).

Like anatomically modern humans, Neandertals had the hunting skill to rank as top predators in diverse climates, adapting their hunting strategies to suit local circumstances (Richards, Pettitt et al., 2000; Bocherens, Drucker et al., 2005; Zilhão, 2006). Both anatomically modern humans and Neandertals left examples of non-figurative “concept-mediated markings” (Bednarick, 1995) on bone, rock, and gravestones (Peyrony, 1934). As early as 75,000 years ago, anatomically modern humans were stringing together beads made from drilled and pierced ostrich eggs and marine shells. By 35,000 years ago, Neandertals were making beads as well, favoring pierced and grooved animal teeth, bone, ivory, soft stone and even fossils (Peyrony, 1934; Bednarick, 1995; d’Errico, Zilhao et al., 1998; Zilhão, 2006). The earliest recognizable musical instruments—flutes made of bird bone, found at Geissenklösterle, have been dated between 33,500 and 37,000 years BP (Hahn and Münzel, 1995; Conard and Uerpmann, 2000).

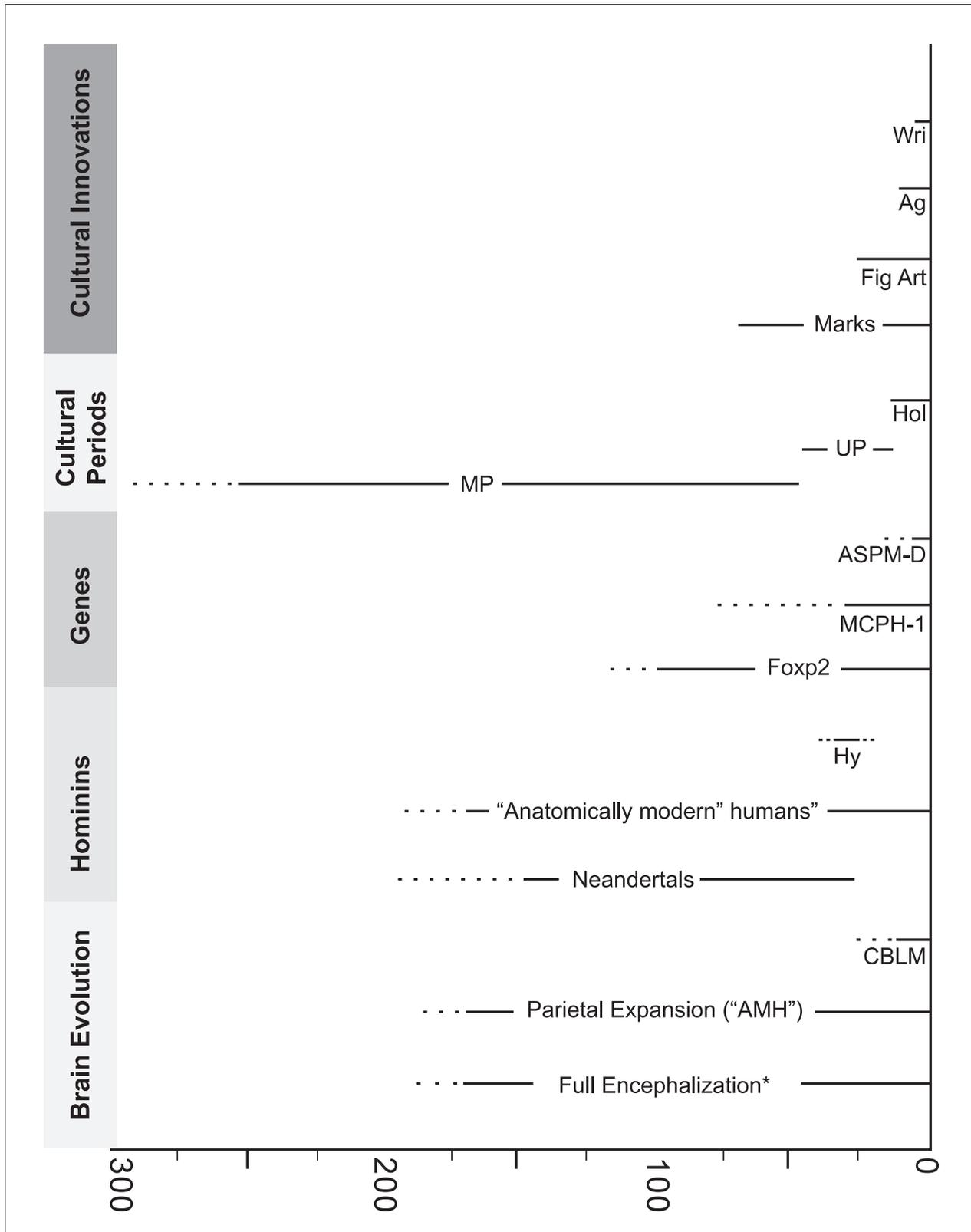


Figure 2. Timetable of Cognitive Developments and Cultural Stages for the Late Pleistocene. Key to abbreviations: "AMH" = anatomically modern humans; "CBLM" = relative cerebellar expansion; "MCPH1" = microcephalin variant MCPH1; "ASPM" = ASPM haplotype 63; "Hy" = period of probable hybridization between Neandertals and anatomically modern humans in Europe; "MP" = Middle Paleolithic cultural period; "UP" = Upper Paleolithic cultural period; "Hol" = Holocene epoch; "Marks" = appearance of "concept-mediated marking" (Bednarick 1995); "FigArt" = appearance of figurate/representational art; "Ag" = onset of agriculture in Western Asia; "Wri" = appearance of writing.

That is to say, Neandertals and anatomically modern humans cannot be distinguished on the basis of their technological accomplishments or behavioral repertoires. Despite marginal differences in encephalization and possible morphological differences related to differential parietal lobe development, there is no uncontroversial evidence that Late Pleistocene anatomically modern humans displayed “advanced” cognitive behavior relative to their Neandertal cousins. This is consistent with the similar cerebellar morphology characteristic of both groups. And it is in accord with the hypothesis that Neandertals and anatomically modern humans were members of the same species.

Introgession of the *microcephalin MCPHI* allele was roughly coincident with early encounters between Neandertals or other archaic humans with the emergence of anatomically modern humans from Africa 50,000–35,000 years BP. Shortly after that time (ca. 30,000 years BP), well-developed figurative art appears in the archeological record. Given the extensive use of ochre and occasional manifestations of “concept-mediated marking” dating back for tens of thousands of years, both in Africa and in Europe, it is reasonable to speculate that the sophisticated drawings, carvings, and small-scale sculptures produced after 30,000 years ago arose from a long-incipient human tendency for visual expression. Newly activated or continued selection acting on the *FOXP2* gene may have contributed to this flowering of symbolic activity. However, increased cerebellar capacity was apparently not a prerequisite for such expressions.

What, then, might account for continued brain evolution in humans after 30,000 years BP, including cerebellar expansion, continued selective pressure acting on *FOXP2*, *MCPHI*, and the appearance and selection associated with *ASPM* haplotype 63?

Climatic stress may have been an important selective agent. Beginning about 28,000 years ago, a period of severe global cooling ensued. Glaciers expanded, forests retreated, and by 18–20,000 years ago, northern Africa was an extreme tropical desert. Steppe-tundra covered those portions of southern Europe that remained unglaciated.

Proliferating technology kept pace with the intensifying cold and shift in ecology: the archeological record from the terminal Pleistocene in Europe includes cordage, woven goods; and eyed needles, fishhooks, weirs, traps, armatures, and projectile weapons such as the atlatl and, later, the bow (Straus, 1995; Straus, 1997; Soffer, 2004). Figurative statuary and cave art continued to flourish during this period as well. Innovations developed to meet extreme conditions were not lost when the glaciers retreated.

By the terminal Pleistocene, humans had achieved a degree of precise motor control, advanced concrete operational intelligence, and a sophisticated, complex, proto-modern material culture (Wynn, 1985; Wynn, 1991; Wynn, 1996). Even the most conservative researchers agree that terminal Pleistocene and early Holocene humans had already developed syntactical

language (Conkey, 1987; Klein, 1992; Noble and Davidson, 1996).

However, they may not have fully developed the formal operational intelligence (characterized by abstract thinking) (Inhelder and Piaget 1958) that is achieved during adolescence and early adulthood in modern humans in contemporary societies. The capacity for formal operational intelligence (and concomitant enhancement of cortico-cerebellar circuitry) may have emerged as a cognitive tool in response to population pressures and/or subsistence strategies related to plant and animal domestication. Early evidence of pastoralism and horticulture are associated with the Younger Dryas, ca. 10,500 years BP (Bar-Yosef, 1998). The earliest towns began to coalesce about 8,000 years ago (Göktürk, Hillegonds et al., 2002). Complex, abstract “external memory devices,” including calendars and notation systems, (Donald, 1993) appeared shortly thereafter.

The cultural context for human cognition changed slowly, but drastically. Formalized power structures, tribal networks, and kinship systems required greater impulse control, deferred gratification, and social cognition. The relentless, complex demands of growing crops and maintaining herds required *abstract* operational intelligence, impulse control and long-term planning that were qualitatively different from the *concrete* operational intelligence, patience, wiliness and observational acuity needed by foragers.

The balance between personal memory and culturally distributed memory shifted. Non-iconographic counting tokens from Sumeria date back 8,000 years, followed by fully developed writing systems by 5,300 years ago (Schmandt-Besserat, 1996). Calendars, accounting systems, formalized liturgies and rituals, legal systems, and epic literature blossomed thereafter.

The specialized cognitive demands placed on terminal Pleistocene and Holocene humans may have favored restructuring of neural computational networks, either ontologically, phylogenetically, or both.

## TERMINAL PLEISTOCENE AND HOLOCENE COGNITIVE SKILLS

If natural selection did in fact operate to change neural circuitry in terminal Pleistocene and Holocene humans, such selection would have been constrained by the need to preserve existing primary brain functions. A “language organ” or “abstract thinking organ” cannot be simply inserted into an unused gyrus or sulcus at an arbitrary point in development. New or enhanced functions emerge based on previously-established neural circuitry.

Phylogenetic changes in the rate or timing of organic development occur through an evolutionary dynamic known as heterochrony. Peramorphosis is a form of heterochrony that involves terminal extension of the latest phase of maturation. In the human brain, the period of late maturation involves vigorous synaptic pruning in the cerebral cortex, accompanied by an increase in

subcortical volume due to myelination and expansion of subcortical circuitry. Peramorphosis is a credible mechanism to explain putative cognitive and neurological differences between recent humans and their Terminal Pleistocene and Holocene predecessors. For example, ontogenic shifts in the timing and duration of cortical growth and subsequent pruning can have significant effects on IQ (Shaw, Greenstein et al., 2006).

The protracted phase of brain maturation during adolescence in modern humans is correlated with a shift in cognitive and psychological strategies in which the cerebellum participates. This shift in cognitive strategies appears to reflect more efficient neural organization and sharing of information among cortical and subcortical brain regions (Katz and Steinmetz, 2002). Behaviorally, the late phase of brain maturation results in the capacity for formal operational thinking, greater voluntary control of behavior, cognitive flexibility, social identity formation, and an enhanced ability to fine-tune cortical activity (Giedd, Snell et al., 1996; Luna, Thulborn et al., 2001; Giedd, 2004; Blakemore and Choudhury, 2006; Shaw, Greenstein et al., 2006). In tasks that require voluntary control of reflexive/impulsive response tendencies, adults exhibit reduced reliance on the neocortex and greater recruitment of the cerebellum than adolescents do (Luna, Thulborn et al., 2001).

## SUMMARY

Given the present evidence, it is impossible to state exactly where or when cerebellar proportions changed during the last 28-30,000 years; whether the change was gradual or rapid; what specific cultural innovations may have been involved; or in what population(s) it first occurred.

However, the data we do have and the correlations that have been observed can be useful in generating hypotheses for future research. For example, cognitive shifts related to cultural behaviors in Terminal Pleistocene and Holocene humans can be explained by peramorphosis. Regulatory changes in genes such as *microcephalin MCPHI* and *ASPM* haplotype 63 that affect brain development might have led to an extended period of circuit-formation and neuronal pruning involving cortico-cerebellar circuitry in response to cognitive demands emerging from cultural intensification. In recent humans, the late adolescent period of brain development coincides with maturation of social cognition and conceptual thinking skills that appear to distinguish us from our terminal Pleistocene and early Holocene forebears.

Additional data are needed related to the timing of cerebellar development, circuit enhancement, neocortical pruning, and cerebellar plasticity. Further sampling will help to establish a range of variation in relative cerebellar volume in early modern humans and contemporary populations. Further genetic comparisons, based on the soon-to-be sequenced Neandertal genome, along with a greater understanding of how *microcephalin*,

*ASPM*, and *FOXP2* affect cerebellar and neocortical development will be important in clarifying the genetic and cultural dynamics that nurtured modern human cognitive potentials.

Cerebellar evolution, regulated by genetic mutation under the influence of complex selective pressures, may well have enabled recent humans to achieve increased cognitive efficiency without a costly increase in overall brain size.

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