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SYNTHESIS PAPER

Brain Size Growth and Life History in Human Evolution

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Abstract Increases in endocranial volume (a measure of brain size) play a major role in human evolution. Despite the importance of brain size increase, the developmental bases of human brain size evolution remain poorly characterized. Comparative analyses of endocranial volume size growth illustrate that distinctions between humans and other primates are consequences of differences in rates of brain size growth, with little evidence for differences in growth duration. Evaluation of available juvenile fossils shows that earliest hominins do not differ perceptibly from chimpanzees (*Pan*). However, rapid and human-like early brain growth apparently characterized *Homo erectus* at about 1 Ma before present. Neandertals show patterns of brain growth consistent with modern humans during infancy, but reach larger sizes than modern humans as a result of differences in later growth. Growth analyses reveal commonalities in patterns of early brain size growth during the last million years human evolution, despite major increases in adult size. This result implies consistency across hominins in terms of maternal metabolic costs of infancy. Continued size growth past infancy in Neandertals and modern humans, when compared to earlier hominins, may have cognitive implications. Differences between Neandertals and modern humans are implied, but difficult to define with certainty.

Keywords Ontogeny · Paleoanthropology · *Australopithecus* · *Homo erectus* · Neandertals

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Introduction

Evolutionary increases in brain size, typically measured by endocranial volume (ECV), rank among the most important and obvious derived changes in human evolution (Darwin 1859; Dubois 1897; Weidenreich 1941; Pilbeam and Gould 1974; Martin 1983, 1989; Rightmire 2004; Schwartz et al. 2004; Neubauer and Hublin 2011). Researchers have noted remarkable variation in endocranical volume (ECV), both through geologic time (Gould and Eldredge 1977; Rightmire 1981; Wolpoff 1986; Leigh 1992a; Schwartz et al. 2004; Falk et al. 2005; Montgomery et al. 2010; Bruner and Holloway 2010) and among contemporaneous taxa [e.g., *Homo floresiensis* and *Homo sapiens* (Falk et al. 2005, 2009; Montgomery et al. 2010)]. Theoretical models of human evolution prioritize brain size, relating evolutionary increases in brain size to myriad variables, including metabolic costs and diet (Martin 1981, 1989; Armstrong 1985; Aiello and Wheeler 1995; Leonard and Robertson 1997; Aiello et al. 2001; Leonard et al. 2003), culture (d' Errico et al. 2009), parturition (Trevathan 1996; Rosenberg and Trevathan 2001; Ponce de Leon et al. 2008), and life history (Harvey et al. 1987; Leigh 2004). Furthermore, new analyses provide insights into phylogenetic and ontogenetic shifts in brain shape (Gunz et al. 2010; Neubauer et al. 2010; Gunz et al. 2012), generating novel theoretical questions about patterns and processes of human brain evolution.

Studies linking evolution and development of the brain are fundamental to understanding human brain evolution. Widely applied models that address the metabolic costs of the human brain (e.g., Aiello and Wheeler 1995; Leonard and Robertson 1997; Aiello et al. 2001; Leonard et al. 2003) are intrinsically ontogenetic, and this may be particularly important when considering total metabolic costs

of the human brain [with estimates ranging from up to 36% of infant metabolic costs (Holliday et al. 1967) and 16–25% of total costs in adults (Aiello and Wheeler 1995; Leonard and Robertson 1997)]. Therefore, selection pressures may target genes affecting metabolic efficiency and brain size at any age. Variable costs during ontogeny further suggest that combinations of individuals can help meet metabolic costs of brain size growth, including mothers, the growing individual itself, or other group members (Leigh 2004). Consequently, brain growth patterns may have important implications for understanding social evolution.

Unfortunately, studies linking phylogenetic to ontogenetic changes in ECV remain rare, mainly because of difficulties in studying juvenile fossils (Dart 1925; Alemseged et al. 2006). Evolutionary developmental perspectives contribute to analyses of human brain evolution because ontogenetic data reveal the factors that ultimately produce adult brain sizes and shapes. Moreover, developmental data provide insights into cognition (Coqueugniot et al. 2004), and can be coupled with genetic data (Dorus et al. 2004; Evans et al. 2004b, 2005, 2006; Gilbert et al. 2005; Mekel-Bobrov et al. 2005, 2007; Vallender and Lahn 2006). Taken together, ontogenetic data offer fundamentally important lines of inquiry into human brain size evolution.

The main objective of this analysis is to investigate the evolutionary history of human brain size growth patterns, measured by ECV, through comparative analyses of chimpanzees (*Pan troglodytes*) and fossil hominins. This analysis complements Neubauer and Hublin's recent overview (2011) by focusing on the details of brain size growth and considering implications of size growth for human life history evolution, cognition, and genetics.

In this study, endocranial volume (ECV) includes the brain and all associated soft tissues, and is used throughout this analysis synonymously with "brain size." Thus, "brain size growth" refers only to size increases in ECV or mass. Analyses test basic hypotheses about patterns of brain size growth in human evolution in order to explore possible relations between brain size growth, maternal metabolism, and life history (Leigh 2004; Leigh and Bernstein 2006). The first hypotheses predict that the large brain of contemporary humans evolved through change in a single size growth "parameter," which would include either an increase in the duration of human brain size growth, or an increase in the rate of brain size growth. A logical alternative is that more complex changes in brain size growth drive brain evolution, possibly through combined changes in rates and durations of brain size growth (see Leigh 1992b, 1994; Leigh and Shea 1996).

These hypotheses have different implications for understanding brain evolution. Thus, this analysis explores developmental processes that lead to evolutionary alterations of adult brain size within a comparative phylogenetic framework. Even with limited data, analyses document a dynamic history of brain size growth in the human lineage, with potentially important life history, cognitive, and genetic correlates. These correlates may reflect differences among hominin life histories, and provide tentative insights into causes of human brain size evolution.

Theoretical Context for Evolution, Development, Life History, and the Human Brain

Growth in brain size during the first few years of primate postnatal life generates high metabolic costs, especially given the large relative size of the neonatal brain (Aiello and Wheeler 1995; DeSilva and Lesnik 2008). Therefore, differences in brain size growth among hominins imply the presence of alternative metabolic cost "profiles," or patterns of metabolic costs. These costs may change as the offspring grows. As a result, different brain size growth patterns may require varying allocations of metabolic resources, even if two taxa reach equivalent adult brain size (e.g., different growth rates producing equal adult brain size via differing growth times). Under these circumstances, distinct growth rates could reveal the evolution of alternative distributions of maternal metabolic costs, as observed among nonhuman primates. Specifically, brain size growth patterns in nonhuman primates covary with maternal metabolic costs, relating closely to levels of maternal investment (Leigh 2004; Leigh and Bernstein 2006). On the one hand, mothers of large-brained species typically invest most heavily in the youngest infants. This life history produces "high quality" juveniles, and reflects investment in current offspring over investment in future offspring. On the other hand, relatively small-brained primate species tend to reach adult brain sizes later by growing more slowly for longer periods of time than large-brained taxa. This reveals low investment in current offspring, typically because mothers divert resources to the next offspring.

These contrasting primate patterns have direct and important implications for understanding human brain size growth evolution. More specifically, it can be hypothesized that variation in brain growth patterns among hominins reflect general patterns seen in primates in terms of how mothers distribute metabolic costs (Ponce de Leon et al. 2008). Metabolic costs incurred by offspring, as well as interspecific differences in metabolic cost patterns, are significant, and probably under intense natural selection in both offspring and mothers (Garber and Leigh 1997; Leigh 2004, 2006a; Leigh and Bernstein 2006).

The application of a metabolic cost framework to hominin brain size growth evolution contrasts with

traditional expectations. Specifically, a traditional view predicts that a uniform process drives variation in adult brain size: brain size differences among taxa are seen as products of simple growth period extensions (Sacher 1959; Sacher and Stafffeldt 1974; Barrickman et al. 2008). A traditional model suggests that hominins progressively evolved longer periods of brain size growth through delays in maturation which produce longer brain growth periods (Sacher 1959; Sacher and Stafffeldt 1974; Barrickman et al. 2008).

Developmental data help distinguish between metabolic and "traditional" models, but also offer tentative insights into cognition (Coqueugniot et al. 2004). For example, a very high rate of human brain size growth, both in absolute and relative terms (Count 1947; Martin 1983), suggests cognitive separation of humans from other primates. Rapid attainment of adult brain size is important because locomotion and language reach developmental milestones at about 1 year of age in modern humans. Thus, associations between brain size and shape growth patterns, language, and other distinctly human capabilities have been suggested (cf. Coqueugniot et al. 2004; Neubauer et al. 2010). Furthermore, late brain size growth may reflect a developing system exposed to environmental stimuli (Black et al. 1987; Greenough et al. 1987; Kramer et al. 2004; Markham and Greenough 2004). In contrast, condensed brain growth periods may reflect limited periods of environmental exposure.

Finally, several studies have identified alleles associated with brain size growth, providing ways to integrate fossil and genetic data. Most importantly, fossil data enable predictions about the antiquity of alleles that generate modern human brain size growth patterns. An understanding of phenotypic differences among human ancestors in terms of brain size growth trajectories will be critical to inferring the timing and effects of genetic evolution in "brain size growth alleles." Such data are also important in addressing genetic hypotheses regarding introgression of alleles from extinct populations, particularly Neandertals (Dorus et al. 2004).

Brain Size Growth in Hominin Evolution

This analysis tests several hypotheses, beginning with a test of the traditional hypothesis that differences in brain size between *Pan* and contemporary *Homo* mainly result from alteration mainly in a single size growth parameter, the duration of brain size growth (Sacher 1959; Sacher and Stafffeldt 1974; Allman et al. 1993; Allman and Hasenstaub 1999; Leigh 2004). Second, hypotheses about differences in patterns of brain size growth among fossil hominins are tested. Following previous analyses of specific hominin taxa (Coqueugniot et al. 2004; Hublin and Coqueugniot 2006; Leigh 2006b; Ponce de Leon et al. 2008), differences in patterns of brain size growth among taxa are expected, such that adult brain sizes in different hominin taxa result from variable ontogenetic processes. More simply, it can be expected that differences interspecific differences in brain size across hominins result from differences in rate of brain size growth, duration differences, or some combination of rate and duration differences (cf. Leigh 1992b). These hypotheses are tested using both endocranial volume estimates and new approximations of pelvic dimensions (which offer approximations of neonatal head sizes) (e.g., Ponce de Leon et al. 2008; Simpson et al. 2008; Weaver and Hublin 2009; Berge and Goularas 2010; Ruff 2010).

Materials and Methods

Materials

Modern human data derive from Marchand's (1902) records of European autopsies from the late 1800s. Marchand attended hundreds of autopsies, extracting the brain and associated soft tissues as soon as possible after death. He then weighed extracted tissues, without attempting to dissect out various structures (brain, meninges, blood vessels, blood, and cerebrospinal fluid). These data are thus ideal for paleoanthropological comparisons because Marchand's mass estimates probably capture the total contents of the endocranium, suggesting that these measures compare favorably to endocasts and endocranial volumes. Marchand's data have been compared to recent MRI-derived data, which include children ranging in age from 4 years to adulthood (Giedd et al. 1996) (not shown in the interest of brevity). The MRI volume data do not include the meninges and associated soft tissues, and thus show lower values than Marchand's data. But, both data sets are compatible, and MRI data may reveal that children are close to adult values as early as 4–5 years of age, which is slightly earlier age at attainment of adult size in Marchand's data (see below).

Chimpanzee brain size data, usually from mass estimates, derive from several sources (Vrba 1998; Leigh 2004), and enable comparisons between chimpanzees and hominin taxa. Moreover, comparisons between chimpanzees and fossil hominins permit assessments of the antiquity of human brain growth patterns. Unfortunately, chimpanzee brain size estimates are vastly less than optimal, and it must be kept in mind that contemporary chimpanzees probably do not simply reflect an ancestral form. Chimpanzee data are also from captives (see Leigh 2004). A core set of chimpanzee brain masses from the Yerkes National Primate Research Center is used in the present study (Herndon et al. 1999). Otherwise, values reported by Vrba (1998) and a

variety of sources she compiled are used. For the current study, these data were extracted from Vrba's study (see procedures in Leigh 2004; unfortunately, a fire destroyed Vrba's data set [pers. comm., 2003]). Recent analyses by Sakai et al. (2011) present MRI data for chimpanzees, and document slow rates of prefrontal white matter development in chimpanzees.

Estimates of hominin (fossil and modern) and nonhuman primate brain size (equated with endocranial volume or ECV) are derived largely from published sources (Table 1, see also comparative data from Barrickman et al. 2008; Isler et al. 2008; Isler and van Schaik 2009; Neubauer et al. 2010; Gunz et al. 2010). The sample size of juvenile fossil specimens is small, although virtual reconstructions have significantly increased samples (McNulty et al. 2006; Ponce de Leon et al. 2008; Simpson et al. 2008; Gunz et al. 2009, 2010; Neubauer et al. 2010).

Taxonomically, juvenile endocranial volume estimates are available for two *Australopithecus afarensis* individuals and the Taung specimen (*A. africanus*). Only a single specimen, Mojokeroto, is available for assessing brain ontogeny in *Homo erectus*, while several Neandertal juvenile and subadult specimens (N = 11) are available [obtained from Ponce de Leon et al. (2008)] and cross-checked with original sources). White et al. (2003) provide data for early modern humans from Herto, dating to about 160,000 years before present. Additional information about fossil brain growth can be derived from pelvic dimensions enabling estimates of brain size at birth. These data derive from several fossil taxa, including *Australopithecus africanus* [STS 14, (Berge and Goularas 2010), *Homo erectus* [Gona (Simpson et al. 2008; Ruff 2010), KNM WT 15000 (Walker and Ruff 1993)]] and Neandertals [Tabun I (Weaver and Hublin 2009; Ponce de Leon et al. 2008)] (see also DeSilva and Lesnik 2008).

The measure "brain size" includes endocranial volume from fossils and mass from necropsies and autopsies. ECV and mass are equalized by multiplying ECV by the specific gravity of brain tissue (1.036) (Hofman 1993). Estimates of brain size, either calibrated by brain mass or endocranial volume, have several inherent limitations that have been discussed extensively (Tobias 1970; Gould 1981; Leigh 2004). Problems include inconsistencies in dissection, possible complications of pathology in autopsy and necropsy data (especially for young individuals), variation in estimating volume (e.g., either by weight or displacement), and so on (see Neubauer and Hublin 2011 for additional information). Other difficulties, characteristic of measuring fossils (Schwartz et al. 2004), also obtain, including possible errors of virtual reconstruction (e.g., Ponce de Leon et al. 2008). Problems of developmental age estimation are also present in the data, particularly for fossils (Coqueugniot et al. 2004). The inherent lack of longitudinal data for most samples poses additional difficulties. Despite these complications, it should be noted that the magnitudes of ontogenetic and phylogenetic changes in the human lineage are so large that they minimize serious problems owing to many sources of measurement error. As with any other fossil data sets, offsetting these problems relies on judicious interpretation of results, as well as explicit recognition that inferences based on these data are tentative and may be speculative. Finally, fossil, autopsy, and necropsy data are all limited by the "osteological paradox" (Wood et al. 1992). This means that inferences about

Table 1 Fossil specimens analyzed

Taxon	Specimen	Reference
Australopithecus afarensis	Dikika-1	Alemseged et al. (2006)
A. afarensis	AL 333-105	Alemseged et al. (2006)
A. africanus	Taung	Dart (1925)
Homo erectus	Mojokerto	Coqueugniot et al. (2004)
Neandertal	Mezmaiskaya	Ponce de Leon et al. (2008)
Neandertal	Dederiyah 1	Ponce de Leon et al. (2008)
Neandertal	Dederiyah 2	Ponce de Leon et al. (2008)
Neandertal	Pech de l'Aze	Ponce de Leon et al. (2008)
Neandertal	Subalyuk	Ponce de Leon et al. (2008)
Neandertal	Roc de Marsal	Ponce de Leon et al. (2008)
Neandertal	Engis2	Ponce de Leon et al. (2008)
Neandertal	La Quina H18	Ponce de Leon et al. (2008)
Neandertal	Teshik Tash	Ponce de Leon et al. (2008)
Neandertal	La Moustier 1	Ponce de Leon et al. (2008)
H. sapiens	European	Marchand (1902)
H. erectus	Gona Pelvis	Simpson et al. (2008)
Neandertal	Tabun Pelvis	Weaver and Hublin (2009)

evolution in the fossil record are based on deceased segments of populations. These segments often have not contributed genes to future generations (e.g., deceased juveniles), and may present anatomical variants that responded negatively to selection. Thus they may not adequately represent genotypes and phenotypes of individuals who left descendants "chosen" by selection.

Age estimates for fossils are based on a variety of techniques. Most age estimates use dentition, which traditionally refer to modern human standards. For this research, estimates follow the judgment of original investigators, which may introduce error (Table 1). For Mojokerto, Coqueugniot et al.'s (2004) estimate of about 1 year of age (human standard) is used. Various age estimates are available for this specimen (see Antón 1997). In addition, the geological context of this specimen is currently under review (Kappelman and Nachman 2010) with preliminary reports indicating a much later age than the 1 Ma estimated by Swisher and colleagues (Swisher et al. 1996). Despite this later age estimate, the fossil is still regarded as *Homo erectus*, and should offer some indication of brain growth in that taxon. Finally, brain size and age estimates for Neandertals are based on analyses by Ponce de Leon et al. (2008), with values digitized from their Fig. 1. It should be noted that age estimates for Neandertals are debated, and recent research indicates that Neandertals may erupt teeth earlier than modern humans (Smith et al. 2007), with some differences in structure (Guatelli-Steinberg et al. 2007) Consequently, Neandertals may be younger than modern humans with comparable sets of dentition. Inferences based on the data can generally adjust for this by assuming earlier ages for Neandertals (essentially, shifting Neandertal data points to earlier ages).

Methods

Estimates of brain weight (g), including converted ECV, and developmental age (in years) are plotted in bivariate space for several comparisons. These plots enable qualitative assessments of taxonomic differences in brain size growth, with fossil taxa plotted along with both chimpanzee and human brain size data. The focus of this study is on absolute brain dimensions, not proportional values, which may provide different insights (Hublin and Coqueugniot 2006; Ponce de Leon et al. 2008). Overall descriptions of brain size growth are derived from nonparametric lowess regression (Cleveland 1979; Cleveland and Devlin 1988; Leigh 1992b). This regression technique provides localized fits to data, unconstrained by parameters, with regressions calculated in Systat 11. Both fossil and modern human values are assessed relative to the position of the estimated lowess regression line. Previous analyses of modern human data have developed parametric models for these data (Jolicoeur et al. 1988), yielding results consistent with nonparametric descriptions.

Results

Chimpanzee-Human Comparisons

Differences in the rate of growth produce adult brain size contrasts between chimpanzees and humans (Fig. 1). Specifically, human brain size growth rates exceed chimpanzee brain size growth rates throughout postnatal ontogeny, including the first year (Count 1947) (Fig. 1, inset). Brain sizes for the two species do not overlap, with differences

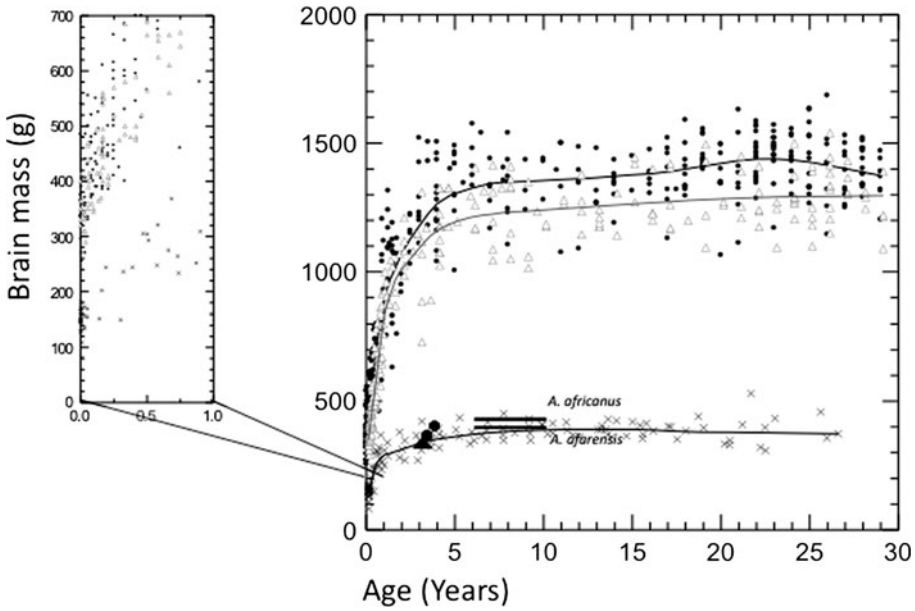

Fig. 1 Brain size growth data for *H. sapiens* (male = *filled circle*, female = *unfilled triangle*), *Pan troglodytes* (×), and *Australopithecus* (Dikika 1 = *filled triangle*, A.L. 333–105 = *filled square*, Taung = *expanded* +). *Lines* represent means for *A. africanus* and *A. afarensis*. *Inset* illustrates human and chimpanzee data for birth through 1 year of age. *Regression lines* are estimated through lowess regression

apparent at birth. Growth curves for both species generally decay. Small increases in growth rates are evident in the human data, comprising "growth spurts" for both males and females, but such spurts are not evident in the chimpanzee data (bearing in mind limits of the chimpanzee data set). As noted, human MRI data are generally compatible with autopsy data (not shown), and Sakai et al. (2011) find parallel rate distinctions in prefrontal white matter development.

Differences in the duration of growth are evident between chimpanzees and humans, but the degree of difference in brain size growth duration is very difficult to measure. Specifically, lowess regressions for human autopsy data show that human brain size is attained by about 6–7 years of age. This concurs with earlier parametric regression estimates based on these data, around 7 years of age (Jolicoeur et al. 1988). Human MRI data suggest an earlier age at growth cessation, with adult values very common among 4- to 6-year-old individuals (Giedd et al. 1996). The age at which brain size growth ceases in chimpanzees is even more difficult to assess, but it may not differ substantially from the age at growth cessation in humans. The fact that species differences in the duration of brain growth between these taxa are difficult to detect is important, and makes clear that rate differences are primary in producing interspecific variation.

Human brains are sexually dimorphic in size, and size dimorphism is established by a combination of sex difference in rates of growth, and a slight difference in the duration of brain size growth. Specifically, female brains grow slower and for a slightly shorter period of time than male brains. Unfortunately, chimpanzee data do not allow firm inferences about the ontogeny of dimorphism, precluding assessments regarding finer points of growth rate variation.

Australopithecus

Brain sizes for the three available juvenile *Australopithecus* specimens fall within the range of variation for chimpanzees (Fig. 1). Pelvic dimensions are comparable with chimpanzees (Berge and Goularas 2010), suggesting consistency in neonatal brain size among taxa. Estimates of fossil juvenile *Australopithecus* brain sizes are far from human values. Assuming different developmental ages does not change this inference appreciably: shifting estimates by 1 year, either negatively or positively, would still show that *Australopithecus* brain sizes overlap those of chimpanzees. With so few data points, it is not possible to establish further similarities between *Australopithecus* and either chimpanzees or humans. In other words, the specifics of *Australopithecus* brain size increase cannot yet be determined, except to say that these three juveniles, spanning roughly 3–6 years of age, overlap with chimpanzee values. Mean values for *A. afarensis* and *A. africanus* fall within the range of chimpanzee variation, although *A. africanus* mean brain size falls above the chimpanzee lowess regression line.

Homo erectus

The Mojokerto specimen, representing juvenile *Homo erectus*, had a brain size comparable to values observed for modern humans at 1 year of age, falling far outside the range of chimpanzee variation (Fig. 2). More specifically, Mojokerto overlaps with modern humans, and lies within the 95% prediction intervals for modern human males [and happens to lie on the lower 95% prediction interval for females (Fig. 3)]. A small number of modern human values older than Mojokerto are actually smaller than Mojokerto.

Average values for early *Homo erectus* and late *Homo erectus* show small differences between Mojokerto's brain size and adult averages. Mojokerto's brain size exceeds brain sizes for several early adult *Homo erectus* specimens, and thus Mojokerto's proportional brain size (e.g., Mojokerto divided by an adult average size) is quite high, as is expected given the small differences between the Mojokerto estimate and adult means (Coqueugniot et al. 2004; Hublin and Coqueugniot 2006). These data suggest minimal brain size increases after 1 year of age in *Homo erectus* (Neubauer and Hublin 2011).

The pelvic outlet of the Gona pelvis is comparable in size to modern humans (Simpson et al. 2008; cf. Walker and Ruff 1993), implying that *H. erectus* could accommodate a neonate with a brain compatible with the size of modern humans. Consequently, the amount of brain growth occurring between birth and 1 year of age (represented by

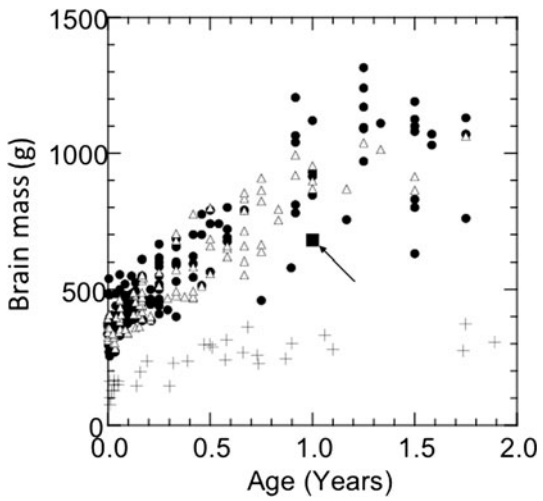

Fig. 2 Brain size growth data for Mojokerto (*filled square*), *H. sapiens* (male = *filled circle*, female = *unfilled triangle*), and *Pan troglodytes* (+)

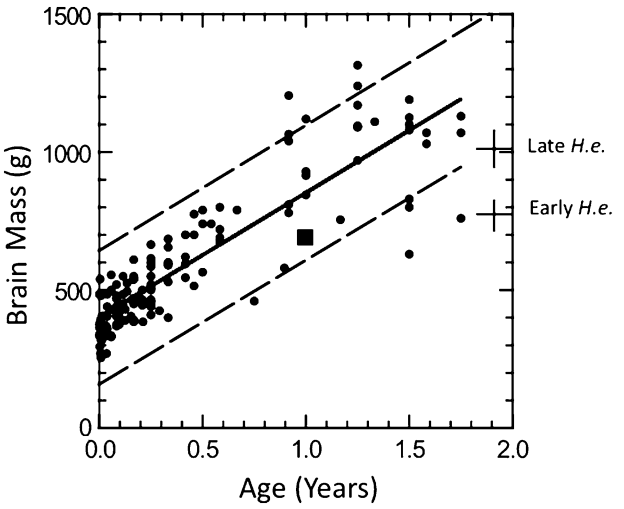

Fig. 3 Ordinary least-squares regression line (*solid*) and 95% confidence intervals (*dashed*) for modern human male brain size growth data. Mojokerto (*filled square*), *H. sapiens* (male = *filled circle*)

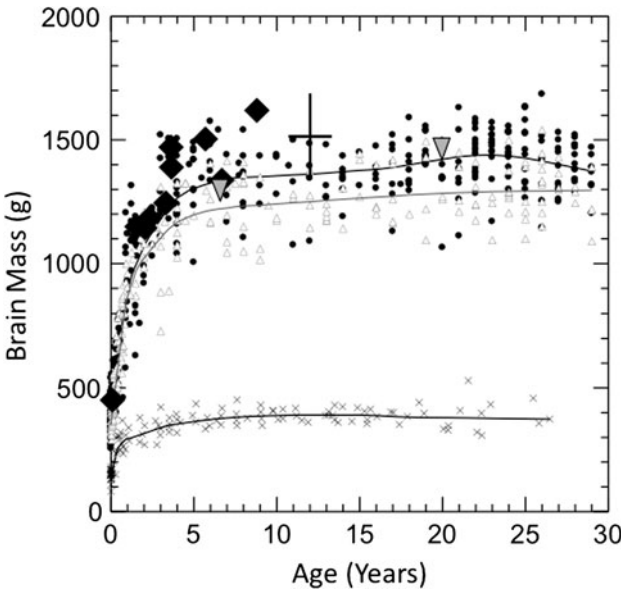

Fig. 4 Brain size growth data for *H. sapiens* (male = *filled circle*, female = *unfilled triangle*), Neandertals (*diamonds*), Herto specimens (*inverted gray triangle*) and *Pan troglodytes* (×). *Regression lines* are estimated through lowess regression. The *horizontal black line* shows the Neandertal adult mean (sexes combined), *vertical line* shows the Neandertal standard deviation (sexes combined)

Mojokerto) would have been very similar to the amount of change in modern humans (Leigh 2006b).

Neandertals and Early Modern Humans

Comparisons between Neandertal and modern human juvenile brain sizes are complicated, with suggestions of shared similarities as well as differences (see also Ponce de Leon et al. 2008). Specifically, the youngest Neandertals fall well within the range of variation for like-aged modern humans (Fig. 4). Similarly, a second group of Neandertals (around 2–4 years of age) also falls within the range of human variation, and in fact, these data points are close to the human lowess regression lines. However, a cluster of older Neandertal juveniles lies above the modern human male lowess regression, while still occupying the range of modern human variation. Among modern humans, variation in the 3- to 6-year-old age group is very high, thus accommodating the Neandertal data points. The Neandertal mean (sexes combined) exceeds the modern human adult male mean, although the lower limit of the Neandertal standard deviation overlaps with the adult modern male human lowess regression line (Fig. 4). Means for adult modern human males and the Neandertal combined sexes mean do not overlap. Finally, early modern humans from Herto present values similar to contemporary modern humans. The Herto juvenile (BOU-VP-16/5), at 6–7 years of age, falls within the human scatter, as does the adult BOU-VP-16/1 (White et al. 2003).

Conflicting alternative hypotheses have been proposed regarding the mechanisms and dimensions of the Neandertal birth canal, with controversy surrounding rotational birth based on the Tabun pelvis (Weaver and Hublin 2009; Ponce de Leon et al. 2008). Regardless of the specifics of birth, the dimensions of the Neandertal birth canal apparently could accommodate a neonatal head similar in size to that of modern humans, suggesting that differences in brain size between Neandertals and modern humans resulted mostly from postnatal growth.

The overall picture that emerges from comparisons of Neandertals and modern humans is that the Neandertal adult brain is larger than the brain of modern humans mainly because of contrasts during late growth. Early periods of brain growth are similar, and this result seems to be robust to the assumption of even earlier estimates of Neandertal ages-at-death (shifting Neandertal data points to the left). However, the larger size of the brain in older juvenile Neandertals ultimately translates to larger adult average brain size. Unfortunately, with the limited data available, it is not possible to determine whether taxonomic differences arise because of brain size growth rate differences, brain size growth duration differences, or some combination of these processes. The larger size of juvenile Neandertal brains suggests that growth rate differences account for the size distinctions between Neandertals and modern humans, but a longer growth period cannot be excluded.

Discussion

In the broad picture, brain sizes of later hominins, probably members of the genus *Homo*, exceed the sizes of

chimpanzee brains because hominin brains grow at higher rates. Moreover, contrasts in brain size growth trajectories among hominins may reveal differences in metabolic costs, and possibly, in life history, cognition, and genetics. Inferences about distinctions among hominins are necessarily tentative. However, a foundation of information about comparative brain size growth in primates can support tentative scenarios and additional hypotheses.

Chimpanzee-Human Differences

The finding that differences in the rate of brain size growth distinguish humans from chimpanzees is fundamentally important (see also Sakai et al. 2011). Specifically, this result contradicts previous hypotheses about the causes of brain size differences between humans and other primates. Traditional ideas about the distinctions in brain size between humans and other taxa stem from Sacher's pioneering research (1959) linking brain size and longevity. Specifically, Sacher argued that greater "precision of physiological regulation" of metabolism, "directly related to encephalization" (1959:128), translated to longer life spans. This further implied linkages of brain size to all life history traits and phases, including age at maturation and total lifespan. We now know that Sacher's insightful interpretation (Sacher 1959; Sacher and Stafffeldt 1974) is incompatible with contemporary models of aging, which generally focus on antagonistic pleiotropy and cellular-level processes (Williams 1957; Shattuck and Williams 2010), which contradict the idea that direct neural control of physiological processes controls aging.

In light of these ideas, the present results, showing that human-chimpanzee differences arise mainly through differences in brain size growth rates, challenge models linking brain size to delayed maturation and thus to long learning periods. Instead, humans and chimpanzees fall within a spectrum of variation in the ways that primate brains reach adult sizes (Leigh 2004). It can be noted that endocranial shape growth differs between chimpanzees and humans (Neubauer et al. 2010; Neubauer and Hublin 2011), joining evidence from white matter studies (Sakai et al. 2011) that chimpanzee-human differences cannot be explained simply by extending human brain size growth periods. Rate differences clearly drive adult brain sizes variation between these taxa.

Fossil Hominins: *Australopithecus*

Ontogenetic data for fossil hominins, while rare, are sufficient to draw several inferences about the evolution of human brain size growth. These data also provide a basis for framing additional hypotheses regarding maternal metabolism, life history, cognition, and developmental genetics, although these hypotheses are somewhat speculative.

Brain sizes of available *Australopithecus* juveniles match the brain sizes of like-aged chimpanzees, and distinctions between the adults of these taxa are limited. While it is tempting to conclude that brain size ontogeny in *Australopithecus* closely resembled chimpanzee brain size ontogeny, a distinction between these taxa in brain sizes between birth and about 4 years of age in these taxa cannot yet be addressed. It is clear that juvenile *Australopithecus* individuals differ from juvenile humans in terms of brain size, so a conservative inference would be that rapid brain size growth rates during the neonatal period are associated solely with the genus *Homo* (see also Neubauer and Hublin 2011). This further implies that the high growth brain size rates that distinguish *Pan* and *Homo* probably evolved either during or after the divergence of *Homo* from other hominin taxa.

Fossil Hominins: *Homo erectus*

Brain growth patterns in *Homo erectus* are relatively clear given the apparently young age and completeness of the Mojokerto infant (about 1 year of age at death [Coqueugniot et al. 2004, but see Antón 1997]). The observation that Mojokerto falls within the range of modern human infant absolute brain sizes (Leigh 2006b) strongly suggests that high rates of brain growth characteristic of modern humans evolved very early (about 1 million years before present, given currently accepted dates for Mojokerto). Moreover, general compatibility in pelvic outlet size between *Homo erectus* [e.g., Gona (Simpson et al. 2008)] suggests that the first year of postnatal brain size growth between modern humans and *H. erectus* was remarkably similar, if not virtually identical. This finding implies that the high brain size growth rates characteristic of modern humans, and generally explained as extensions of fetal brain growth rates (Count 1947), are of considerable antiquity.

Fossil Hominins: Neandertals

The Neandertal sample is small but informative regarding brain size growth. This taxon reaches the largest adult brain size in this comparative sample. Differences between Neandertals and modern humans occur in late phases of growth, while early brain sizes matching both *H. erectus* and modern humans. Ponce de Leon et al. (2008) have argued that infant Neandertal brain growth rates exceed those of modern humans. While this is possible based on their studies of proportional size, the current absolute size data do not support that position unambiguously. Consistent with their results, however, older Neandertal juveniles have larger absolute brain sizes than expected for modern humans.

Evolutionary Implications for Maternal Metabolism and Life Histories

Differences in brain size growth trajectories among hominins may have important implications with regard to metabolic costs and life history [see also Gunz et al.'s analyses of shape change in Neandertals (2010)]. Specifically, consistency in the costs of infant brain growth among *Homo* species (*H. erectus*, Neandertals, and modern humans) are implied, but costs late in development evidently differed among these taxa. More specifically, *H. erectus* probably encountered minimal costs of brain size growth after the first year. On the other hand, Neandertals probably faced higher metabolic costs of brain growth later in ontogeny than either *H. erectus* or modern humans.

High neonatal brain growth rates have important implications, given that maternal investment is associated with brain size in primates (Leigh 2004; Leigh and Bernstein 2006). Shared absolute brain size growth patterns during infancy suggest that that *H. erectus*, Neandertals, and modern human faced similar metabolic costs of young infants. Most likely, these costs were borne primarily by mothers. However, costs of brain size growth in *Homo erectus* after the first year were negligible, and probably much lower than in either Neandertals or modern humans.

Variation in *Homo* suggests tentative and somewhat speculative differences in life histories. For example, similarities in brain size growth in the first postnatal year between *H. erectus*, Neandertals, and modern humans, suggest that neonates of all taxa were equally "expensive" in a metabolic sense. However, metabolic costs of brain size growth would not be a factor after the first year for *H. erectus* mothers, probably facilitating investments in subsequent offspring. If *H. erectus* faced relatively high but brief metabolic costs of supporting infant brain growth, then this may also reveal minimal tradeoffs between current and future offspring characteristic of modern humans (Hill and Hurtado 1996; Blomquist 2009; see also Hawkes et al. 1998; Hawkes 2003, 2004). The absence of such tradeoffs may be associated with high rates of population increase without so-called "fast" life histories. While tentative, it can be suggested that the period of intense maternal investment by *H. erectus* was relatively brief, and may not have necessitated the kinds of support networks characteristic of modern humans, and possibly, Neandertals. Mojokerto's ontogenetic pattern reflects reduced tradeoffs between current and future offspring faced by many other organisms. However, such a pattern may have been associated with cognitive limitations, possibly inducing other kinds of tradeoffs (see below).

In contrast to *Homo erectus*, Neandertals seem to have experienced more brain size growth later in development (although, as noted, the specifics remain unclear). Moreover, differences between Neandertals and modern humans suggest contrasts in maternal metabolism and life history between these two taxa.

Neandertal brain size growth is difficult to interpret with reference to comparative primate metabolic models. However, the current findings allow refinements of Ponce de Leon et al.'s inference that brain size growth patterns drove late maturation in Neandertals (2008). Their inference is based on comparative primate data, but the significant size increases of Neandertals are very unusual, so it is difficult to know how far models from comparative primatology can be extended. If mothers helped meet the costs of late brain size brain growth, then this would support late maturation. This could be associated with late weaning (cf. Humphrey 2010), and thus delayed maternal maturation. It should also be noted that such late increases in brain size would favor late maturation even if they occurred after weaning by placing the individual's growth and reproduction into competition. Thus, the overall picture that emerges is that several factors related to brain growth would have favored late maturation in Neandertals. This would, in turn, lead to demographic tradeoffs associated with late reproduction (Blomquist 2009). An estimate of Neandertal weaning age is very important because this would allow inferences about brain growth and maternal costs. Despite uncertainties, the available data do suggest that older juvenile Neandertals were "costly" from a metabolic standpoint. These costs may have had social and cultural consequences that could be reflected in the archaeological record.

Neandertal-contemporary human comparisons also have implications for later evolution of modern humans. Similarities between brain sizes of the Herto hominins and contemporary humans strongly suggest a longstanding human pattern, and could imply that the Neandertal pattern is derived. This further suggests comparatively low maternal metabolic costs for modern humans, possibly representing a factor that limits life history tradeoffs in contemporary humans.

Implications for Cognition and Developmental Genetics

Coqueugniot et al. (2004) argued that the relatively high proportional brain size in the young Mojokerto implied significant cognitive restrictions in *H. erectus*. While inferences cognitive attributes from morphological data are difficult to make with certainty, the present results could suggest a dynamic system in Neandertals and modern humans. Rapid increases in brain size in modern humans from 1 year of age onward are associated with dynamic remodeling of neurons. This remodeling may occur into adulthood (Black et al. 1987; Greenough et al. 1987;

Kramer et al. 2004; Markham and Greenough 2004). Extended growth periods in Neandertals and contemporary humans suggest cognitive distinctions between these taxa on the one hand, and *Homo erectus* on the other.

In terms of developmental genetics, numerous alleles affect brain size growth (Vallender and Lahn 2006). Thus, data on the evolutionary history of brain size growth phenotypes should enable predictions about DNA sequence variation. Based on this study, it appears that alleles promoting rapid early brain growth were established early in *Homo*, and that these alleles differ substantially from alleles that influence brain growth in other primates. Analyses of sequence variation should reveal major changes in "early brain size growth alleles" dating to within 2–2.5 Ma (or within the time span of the genus *Homo*). On the other hand, sequence variation in alleles associated with later brain growth should reveal less variation, indicating a more recent evolutionary history.

Information about Neandertal brain growth phenotypes has important implications for genetic variation in contemporary humans. Specifically, Lahn and colleagues have suggested that introgression of alleles from Neandertal populations facilitated increased modern human adult brain sizes (Vallender and Lahn 2006). The present study indicates that introgressed alleles probably do not account for similarities between Neandertals and humans in early brain size growth, given that *Homo erectus*, Neandertals, and contemporary humans all share the phenotype. Moreover, the Herto fossils are important in this regard, suggesting antiquity of modern human brain size growth without necessary influence of Neandertal introgression.

Conclusions

Comparative investigations reveal complexity in the evolutionary history of hominin brain size growth. The major differences in rates of brain size growth between chimpanzees and contemporary humans imply specific kinds alterations over the course of human evolution involving growth rates. Elevated brain size growth rates indicate that high metabolic costs of juveniles help define the human lineage.

Juvenile fossils, although rare, reveal additional complexity in the evolution of human brain size growth. Available evidence suggests no major distinctions between *Australopithecus* and *Pan troglodytes*, although the data are mute with respect to infant brain size growth. However, the rapid rate of brain growth observed in modern humans may be a phenomenon limited to the genus *Homo*.

Current data for the genus *Homo* reveal that the infant brain size growth pattern in *Homo erectus* was modern-human-like. When coupled with similarities in birth canal dimensions in *Homo erectus*, Neandertals, and contemporary humans, these data suggest that the rapid infant brain growth rate characteristic of modern humans apparently evolved by about 1 Ma. Limited changes in *H. erectus* brain size after 1 year of age imply low later metabolic costs as well as limits on cognitive development.

Neandertals reached the largest brain sizes among these hominin taxa by emphasizing comparatively late brain size growth. The Neandertal brain size growth phenotype suggests that brain size growth patterns imposed high metabolic costs. Finally, an understanding of brain size growth phenotypes among hominins has important implications for understanding the genetics of brain size growth in contemporary humans. Infant growth patterns and associated alleles seem to have been established early in hominin evolution, while control of later brain growth is a more variable and recent evolutionary phenomenon.

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References

Aiello, L. C., Bates, N., & Joffe, T. (2001). In defense of the expensive tissue hypothesis. In D. Falk & K. R. Gibson (Eds.), *Evolutionary anatomy of the primate cerebral cortex* (pp. 57–78). New York: Cambridge University Press.

Aiello, L. C., & Wheeler, P. (1995). The expensive tissue hypothesis. *Current Anthropology, 36*, 199–222.

Alemseged, Z., Spoor, F., Kimbel, W. H., Bobe, R., Geraads, D., Reed, D., et al. (2006). A juvenile early hominin skeleton from Dikika, Ethiopia. *Nature, 443*, 296–301.

Allman, J., & Hasenstaub, A. (1999). Brains, maturation times, and parenting. *Neurobiology of Aging, 20*, 447–454.

Allman, J. M., McLaughlin, T., & Hakeem, A. (1993). Brain structures and life-span in primate species. *Proceedings of the National Academy of Sciences of the United States of America, 90*, 3559–3563.

Antón, S. C. (1997). Developmental age and taxonomic affinity of the Mojokerto child, Java, Indonesia. *American Journal of Physical Anthropology, 102*, 497–514.

Armstrong, E. (1985). Relative brain size in monkeys and prosimians. *American Journal of Physical Anthropology, 66*, 263–273.

Barrickman, N. L., Bastian, M. L., Isler, K., & van Schaik, C. P. (2008). Life history costs and benefits of encephalization: A comparative test using data from long-term studies of primates in the wild. *Journal of Human Evolution, 54*, 568–590.

Berge, C., & Goularas, D. (2010). A new reconstruction of STS 14 pelvis (*Australopithecus africanus*) from computed tomography and three-dimensional modeling techniques. *Journal of Human Evolution, 58*, 262–272.

Black, J. E., Greenough, W. T., Anderson, B. J., & Isaacs, K. R. (1987). Environment and the aging brain. *Canadian Journal of Psychology, 41*, 111–130.

Blomquist, G. E. (2009). Trade-off between age of first reproduction and survival in a female primate. *Biology Letters, 5*, 339–342.

Bruner, E., & Holloway, R. L. (2010). A bivariate approach to the widening of the frontal lobes in the genus Homo. *Journal of Human Evolution, 58*, 138–146.

Cleveland, W. S., & Devlin, S. J. (1988). Locally weighted regression: An approach to regression analysis by local fitting. *Journal of the American Statistical Association, 83*, 596–610.

Cleveland, W. S. (1979). Robust locally weighted regression and smoothing scatterplots. *Journal of American Statistical Association, 74*, 829–836.

Coqueugniot, H., Hublin, J.-J., Veillon, F., Houet, F., & Jacob, T. (2004). Early brain growth in *Homo erectus* and implications for cognitive ability. *Nature, 431*, 299–302.

Count, E. W. (1947). Brain and body weight in man: Their antecedents in growth and evolution. *Annals of the New York Academy of Sciences, XLVI*, 993–1122.

Dart, R. A. (1925). *Australopithecus africanus*: The man-ape of South Africa. *Nature, 115*, 195–199.

Darwin, C. (1859). *On the Origin of the Species by Means of Natural Selection, or, the Preservation of Favoured Races in the Struggle for Life*. London: J. Murray.

d'Errico, F., Vanhaeren, M., Barton, N., Bouzouggar, A., Mienis, H., Richter, D., et al. (2009). Out of Africa: Modern human origins special feature: Additional evidence on the use of personal ornaments in the middle paleolithic of North Africa. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 16051–16056.

DeSilva, J. M., & Lesnik, J. (2008). Brain size at birth throughout human evolution: A new method for estimating neonatal brain size in hominins. *Journal of Human Evolution, 55*, 1064–1074.

Dorus, S., Vallender, E. J., Evans, P. D., Anderson, J. R., Gilbert, S. L., Mahowald, M., et al. (2004). Accelerated evolution of nervous system genes in the origin of homo sapiens. *Cell, 119*, 1027–1040.

Dubois, E. (1897). Ueber die Abhängigkeit des Hirngewichtes von derKörpergrösse bei den Säugtieren. *Archives of Anthropology, 25*, 1–28.

Evans, P. D., Vallender, E. J., & Lahn, B. T. (2006). Molecular evolution of the brain size regulator genes CDK5RAP2 and CENPJ. *Gene, 375*, 75–79.

Evans, P. D., Gilbert, S. L., Mekel-Bobrov, N., Vallender, E. J., Anderson, J. R., Vaez-Azizi, L. M., et al. (2005). Microcephalin, a gene regulating brain size, continues to evolve adaptively in humans. *Science, 309*, 1717–1720.

Evans, P. D., Anderson, J. R., Vallender, E. J., Choi, S. S., & Lahn, B. T. (2004a). Reconstructing the evolutionary history of microcephalin, a gene controlling human brain size. *Human Molecular Genetics, 13*, 1139–1145.

Evans, P. D., Anderson, J. R., Vallender, E. J., Gilbert, S. L., Malcom, C. M., Dorus, S., et al. (2004b). Adaptive evolution of ASPM, a major determinant of cerebral cortical size in humans. *Human Molecular Genetics, 13*, 489–494.

Falk, D., Hildebolt, C., Smith, K., Morwood, M. J., Sutikna, T., Jatmiko, et al. (2009). LB1's virtual endocast, microcephaly, and hominin brain evolution. *Journal of Human Evolution, 57*, 597–607.

Falk, D., Hildebolt, C., Smith, K., Morwood, M. J., Sutikna, T., Brown, P., et al. (2005). The brain of LB1, *Homo floresiensis*. *Science, 308*, 242–245.

Garber, P. A., & Leigh, S. R. (1997). Ontogenetic variation in small-bodied new world primates: Implications for patterns of reproduction and infant care. *Folia Primatologica, 68*, 1–22.

Giedd, J. N., Snell, J. W., Lange, N., Rajapakse, J. C., Casey, B. J., Kozuch, P. L., et al. (1996). Quantitative magnetic resonance imaging of human brain development: Ages 4–18. *Cerebral Cortex, 6*, 551–560.

Gilbert, S. L., Dobyns, W. B., & Lahn, B. T. (2005). Genetic links between brain development and brain evolution. *Nature Reviews Genetics, 6*, 581–590.

Gould, S. J. (1981). *The Mismeasure of Man*. New York: Alfred R. Knopf.

Gould, S. J., & Eldredge, N. (1977). Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology, 3*, 115–151.

Greenough, W. T., Black, J. E., & Wallace, C. S. (1987). Experience and brain development. *Child Development, 58*, 539–559.

Guatelli-Steinberg, D., Reid, D. J., & Bishop, T. A. (2007). Did the lateral enamel of Neandertal anterior teeth grow differently from that of modern humans? *Journal of Human Evolution, 52*, 72–84.

Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G. W., & Bookstein, F. L. (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution, 57*, 48–62.

Gunz, P., Neubauer, S., Maureille, B., & Hublin, J.-J. (2010). Brain development after birth differs between Neanderthals and modern humans. *Current Biology, 20*(21), R921–R922.

Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., & Hublin, J.-J. (2012). A uniquely human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mesmaiskaya. *Journal of Human Evolution*. http://dx.doi.org/10.1016/j.jhevol.2011.11.013.

Harvey, P. H., Martin, R. D., & Clutton-Brock, T. H. (1987). Life histories in a comparative perspective. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 181–196). Chicago: University of Chicago Press.

Hawkes, K. (2004). Human longevity: The grandmother effect. *Nature, 428*, 128–129.

Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology, 15*, 380–400.

Hawkes, K., O'Connell, J. F., Jones, N. G., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America, 95*, 1336–1339.

Herndon, J. G., Tigges, J., Anderson, D. C., Klumpp, S. A, & McClure, H. M. (1999). Brain weight throughout the life span of the chimpanzee. *Journal of Comparative Neurology, 409*, 567–572.

Hill, K., & Hurtado, A. M. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Walter de Gruyter, Inc.

Hofman, M. A. (1993). Encephalization and the evolution of longevity in mammals. *Journal of Evolutionary Biology, 6*, 209–627.

Holliday, M. A., Potter, D., Jarrah, A., & Bearg, S. (1967). The relation of metabolic rate to body weight and organ size. *Pediatric Research, 1*, 185–195.

Hublin, J.-J., & Coqueugniot, H. (2006). Absolute or proportional brain size: That is the question. A reply to comments. *Journal of Human Evolution, 50*, 109–113.

Humphrey, L. T. (2010). Weaning behaviour in human evolution. *Seminars in Cell & Developmental Biology, 21*, 453–461.

Isler, K., & van Schaik, C. P. (2009). The expensive brain: A framework for explaining evolutionary changes in brain size. *Journal of Human Evolution, 57*, 392–400.

Isler, K., Kirk, C. E., Miller, J. M., Albrecht, G. A., Gelvin, B. R., & Martin, R. D. (2008). Endocranial volumes of primate species: Scaling analyses using a comprehensive and reliable data set. *Journal of Human Evolution, 55*, 967–978.

Jolicoeur, P., Baron, G., & Cabana, T. (1988). Cross-sectional growth and decline of human stature and brain weight in 19th-century Germany. *Growth, Development, and Aging, 52*, 201–206.

Kappelman, J., & Nachman, B. A. (2010). Temperate migrations: Climatically-mediated movements north (and south again?). *American Journal of Physical Anthropology, 141*, 139.

Kramer, A. F., Bherer, L., Colcombe, S. J., Dong, W., & Greenough, W. T. (2004). Environmental influences on cognitive and brain plasticity during aging. *The Journals of Gerontology: Series A: Biological Sciences and Medical Sciences, 59*, M940–M957.

Leigh, S. R. (1992a). Cranial capacity evolution in *Homo erectus* and early *Homo sapiens*. *American Journal of Physical Anthropology, 87*, 1–13.

Leigh, S. R. (1992b). Patterns of variation in the ontogeny of primate body size dimorphism. *Journal of Human Evolution, 23*(1), 27–50.

Leigh, S. R. (1994). Ontogenetic correlates of diet in anthropoid primates. *American Journal of Physical Anthropology, 94*, 499–522.

Leigh, S. R. (2004). Brain growth, life history, and cognition in primate and human evolution. *American Journal of Primatology, 62*, 139–164.

Leigh, S. R. (2006a). Cranial ontogeny of *Papio* baboons (*Papio hamadryas*). *American Journal of Physical Anthropology, 130*, 71–84.

Leigh, S. R. (2006b). Brain ontogeny and life history in *Homo erectus*. *Journal of Human Evolution, 50*, 104–108.

Leigh, S. R., & Bernstein, R. M. (2006). Ontogeny, life history, and maternal investment in baboons. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives* (pp. 225–256). New York: Springer.

Leonard, W. R., Robertson, M. L., Snodgrass, J. J., & Kuzawa, C. W. (2003). Metabolic correlates of hominid brain evolution. *Comparative Biochemistry and Physiology: Part A, Molecular & Integrative Physiology, 136*, 5–15.

Leonard, W. R., & Robertson, M. L. (1997). Comparative primate energetics and hominid evolution. *American Journal of Physical Anthropology, 102*, 265–281.

Leigh, S. R., & Shea, B. T. (1996). Ontogeny of body size variation in apes. *American Journal of Physical Anthropology, 99*, 43–65.

Marchand, F. (1902). *Ueber Das Hirngewicht Des Menschen*. Leipzig: B.G. Teubner.

Markham, J. A., & Greenough, W. T. (2004). Experience-driven brain plasticity: Beyond the synapse. *Neuron Glia Biology, 1*, 351–363.

Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature, 293*, 57–60.

Martin, R. D. (1983). *Human brain evolution in an ecological context* (James Arthur Lecture on the Evolution of the Human Brain, no. 52, 1982). New York: American Museum of Natural History.

Martin, R. D. (1989). Evolution of the brain in early homininds. *Ossa, 14*, 49–62.

McNulty, K. P., Frost, S. R., & Strait, D. S. (2006). Examining affinities of the Taung child by developmental simulation. *Journal of Human Evolution, 51*, 274–296.

Mekel-Bobrov, N., Posthuma, D., Gilbert, S. L., Lind, P., Gosso, M. F., Luciano, M., et al. (2007). The ongoing adaptive evolution of ASPM and microcephalin is not explained by increased intelligence. *Human Molecular Genetics, 16*, 600–608.

Mekel-Bobrov, N., Gilbert, S. L., Evans, P. D., Vallender, E. J., Anderson, J. R., Hudson, R. R., et al. (2005). Ongoing adaptive evolution of ASPM, a brain size determinant in homo sapiens. *Science, 309*, 1720–1722.

Montgomery, S. H., Capellini, I., Barton, R. A., & Mundy, N. I. (2010). Reconstructing the ups and downs of primate brain evolution: Implications for adaptive hypotheses and *Homo floresiensis*. *BMC Biology, 8*, 9.

Neubauer, S., & Hublin, J.-J. (2011). The evolution of human brain development. *Evolutionary Biology*. doi 10.1007/s11692-011-9156-1.

Neubauer, S., Gunz, P., & Hublin, J.-J. (2010). Endocranial shape changes during growth in chimpanzees and humans: A morphometric analysis of unique and shared aspects. *Journal of Human Evolution, 59*, 555–556.

Pilbeam, D., & Gould, S. J. (1974). Size and scaling in human evolution. *Science, 186*, 892–901.

Ponce de Leon, M. S., Golovanova, L., Doronichev, V., Romanova, G., Akazawa, T., Kondo, O., et al. (2008). Neanderthal brain size at birth provides insights into the evolution of human life history. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 13764–13768.

Rightmire, G. P. (1981). Patterns in the evolution of *Homo erectus*. *Paleobiology, 7*, 241–246.

Rightmire, G. P. (2004). Brain size and encephalization in early to mid-pleistocene *Homo*. *American Journal of Physical Anthropology, 124*, 109–123.

Rosenberg, K. R., & Trevathan, W. R. (2001). The evolution of human birth. *Scientific American, 285*, 72–77.

Ruff, C. (2010). Body size and body shape in early hominins—implications of the Gona pelvis. *Journal of Human Evolution, 58*, 166–178.

Sacher, G. A. (1959). Relationship of lifespan to brain weight and body weight in mammals. In G. E. W. Wolstenholme & M. O'Connor (Eds.), *C.I.B.A. foundation Colloquia on aging volume 5: The lifespan of animals* (pp. 115–133). London: Churchill.

Sacher, G. A., & Staffeldt, E. F. (1974). Relation of gestation time to brain weight for placental mammals. *American Naturalist, 108*, 593–615.

Sakai, T., Mikami, A., Matsui, M., Suzuki, J., Hamada, Y., Tanaka, M., et al. (2011). Differential prefrontal white matter development in chimpanzees and humans. *Current Biology, 21*, 1397–1402.

Schwartz, J. H., Holloway, R. L., Broadfield, D. C., Tattersall, I., & Yuan, M. S. (2004). *The Human Fossil Record Volume 3, Brain Endocasts - the Paleoneurological Evidence*. Hoboken, NJ: John Wiley and Sons.

Shattuck, M. R., & Williams, S. A. (2010). Arboreality has allowed for the evolution of increased longevity in mammals. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 4635–4639.

Simpson, S. W., Quade, J., Levin, N. E., Butler, R., Dupont-Nivet, G., Everett, M., et al. (2008). A female *Homo erectus* pelvis from Gona, Ethiopia. *Science, 322*, 1089–1092.

Smith, T. M., Toussaint, M., Reid, D. J., Olejniczak, A. J., & Hublin, J. J. (2007). Rapid dental development in a middle paleolithic Belgian Neanderthal. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 20220–20225.

Swisher, C. C., 3rd, Rink, W. J., Antón, S. C., Schwarcz, H. P., Curtis, G. H., Suprijo, A., et al. (1996). Latest *Homoerectus* of Java: Potential contemporaneity with *Homo sapiens* in Southeast Asia. *Science, 274*, 1870–1874.

Tobias, P. V. (1970). Brain-size, grey matter and race–fact or fiction? *American Journal of Physical Anthropology, 32*, 3–25.

Trevathan, W. R. (1996). The evolution of bipedalism and assisted birth. *Medical Anthropology Quarterly, 10*, 287–290.

Vallender, E. J., & Lahn, B. T. (2006). A primate-specific acceleration in the evolution of the caspase-dependent apoptosis pathway. *Human Molecular Genetics, 15*, 3034–3040.

Vrba, E. S. (1998). Multiphasic growth models and the prolonged growth exemplified by human brain evolution. *Journal of Theoretical Biology, 190*, 227–239.

Walker, A., & Ruff, C. B. (1993). Reconstruction of the pelvis. In A. Walker & R. Leakey (Eds.), *The Nariokotome Homo erectus Skeleton* (pp. 221–233). Cambridge: Harvard Univ. Press.

Weaver, T. D., & Hublin, J. J. (2009). Neandertal birth canal shape and the evolution of human childbirth. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 8151–8156.

Weidenreich, F. (1941). The brain and its rôle in the phylogenetic transformation of the human skull. *Transactions of the American Philosophical Society, 31*, 320–442.

White, T. D., Asfaw, B., DeGusta, D., Gilbert, H., Richards, G. D., Suwa, G., et al. (2003). Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature, 423*, 724–747.

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution, 11*, 398–4111.

Wolpoff, M. H. (1986). Stasis in the interpretation of evolution in *Homo erectus*: A reply to Rightmire. *Paleobiology, 12*, 325–328.

Wood, J., Milner, G. R., Harpending, H. C., & Weiss, K. M. (1992). The osteological paradox: Problems of inferring prehistoric health from skeletal samples. *Current Anthropology, 33*, 343–370.