Journal of Human Evolution 81 (2015) 41–47

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

A neonatal perspective on *Homo erectus* brain growth

Zachary Cofran [a, *], Jeremy M. DeSilva [b]

[a] School of Humanities and Social Sciences, Nazarbayev University, 53 Kabanbay Batyr, 010000 Astana, Kazakhstan
[b] Department of Anthropology, Boston University, 232 Bay State Road, Boston, MA 02215, USA

ARTICLE INFO

Article history:
Received 1 August 2014
Accepted 17 February 2015
Available online 12 March 2015

Keywords:
Life history
Resampling
Simulation

ABSTRACT

The Mojokerto calvaria has been central to assessment of brain growth in *Homo erectus*, but different analytical approaches and uncertainty in the specimen's age at death have hindered consensus on the nature of *H. erectus* brain growth. We simulate average annual rates (AR) of absolute endocranial volume (ECV) growth and proportional size change (PSC) in *H. erectus*, utilizing estimates of *H. erectus* neonatal ECV and a range of ages for Mojokerto. These values are compared with resampled ARs and PSCs from ontogenetic series of humans, chimpanzees, and gorillas from birth to six years. Results are consistent with other studies of ECV growth in extant taxa. There is extensive overlap in PSC between all living species through the first postnatal year, with continued but lesser overlap between humans and chimpanzees to age six. Human ARs are elevated above those of apes, although there is modest overlap up to 0.50 years. Ape ARs overlap throughout the sequence, with gorillas slightly elevated over chimpanzees up to 0.50 years. Simulated *H. erectus* PSCs can be found in all living species by 0.50 years, and the median falls below the human and chimpanzee ranges after 2.5 years. *H. erectus* ARs are elevated above those of all extant taxa prior to 0.50 years, and after two years they fall out of the human range but are still above ape ranges. A review of evidence for the age at death of Mojokerto supports an estimate of around one year, indicating absolute brain growth rates in the lower half of the human range. These results point to secondary altriciality in *H. erectus*, implying that key human adaptations for increasing the energy budget of females may have been established by at least 1 Ma.

Introduction

The size and structure of the human brain underlie the remarkable cognitive capabilities requisite for the evolutionary success of our species. At an average of over 1300 g (Hofman and Falk, 2012), the adult human brain is roughly six times larger than expected for a mammal of our body size (Martin, 1981). Brain is an energetically expensive tissue (Aiello and Wheeler, 1995), consuming some 25% of adult humans' resting energy expenditure, and over 60% of infants' (Holliday, 1986; Leonard et al., 2003). The brain not only enables, but also requires, the cultural capacities necessary to energetically sustain it. Identifying the processes and patterns responsible for the growth of this exceptional brain is therefore an important question for human evolutionary developmental biology.

The means by which humans achieve large brain size seems singular in two main ways. First, humans have very high rates of brain size growth during the third trimester of pregnancy (Roelfsema et al., 2004). These rates are absolutely high and accelerate immediately prior to birth, in contrast to those of our closest living relatives (*Pan troglodytes*) whose prenatal rates are always lower than in humans and begin decelerating 10 weeks prior to birth (Sakai et al., 2012). In fact, the high energetic cost of maintaining this pace of brain growth in humans has been hypothesized to be the mechanism that triggers birth itself, as the energetic demands of the fetus outpace what the mother can provide (Dunsworth et al., 2012). The human pattern results in a neonatal brain size of 360–380 g, which is close to the size of an adult chimpanzee brain. However, because of the enormous size of an adult human brain, the actual percentage of adult brain volume achieved by birth in humans is only around 30% of adult values (DeSilva and Lesnik, 2006). Chimpanzee neonates, on the other hand, have absolutely small brains of around 150 g, which corresponds to a higher proportion (40%) of adult values (DeSilva and Lesnik, 2006). So, although humans have relatively small brains at birth, they nevertheless experience high rates of prenatal brain growth given their absolutely larger size.

* Corresponding author.
E-mail address: zachary.cofran@nu.edu.kz (Z. Cofran).

http://dx.doi.org/10.1016/j.jhevol.2015.02.011
0047-2484/

A second exceptional aspect of human brain growth is that very high, fetal-like rates continue during the first 1.5 years of life (Count, 1947; Dobbing and Sands, 1979; Leigh, 2004). This observation has led to the characterization of human neonates as experiencing secondary altriciality (Portmann, 1941), or exterogestation (Montagu, 1971), terms that regard humans as unusual among primates by having *in utero* fetal brain development patterns continue outside the womb. Components of the brain do not expand uniformly during this time, but rather the uniquely high rates appear to be driven by the proliferation of white matter, a pattern not seen in *P. troglodytes* (Sakai et al., 2013). White matter is composed chiefly of myelinated axons, which help make connections between different regions of the brain. Thus, it has been suggested that the first two years of life are critical for establishing the cognitive potential of the human brain (see references in Sakai et al., 2013). In sum, postnatal brain growth both imposes important energetic demands on provisioning parents and growing offspring, and influences the degree to which a growing brain interacts with environmental stimuli. It is therefore of interest to know when this pattern of fetal-like postnatal rates of brain growth emerged in our lineage.

The evolutionary origins of human postnatal brain growth, and its concomitant correlates of life history and maternal energetics, are unclear due to a lack of relevant fossils. Coqueugniot et al. (2004) suggested ape-like brain size growth in *Homo erectus*, based on an estimated age of death around one year for the >1.2 Ma Mojokerto calvaria and a proportional endocranial volume (ECV) of 70–80% of the early *H. erectus* adult mean. O'Connell and DeSilva (2013) used larger samples of *H. erectus* adults and found Mojokerto's proportional ECV to fall within an extensive range of overlap between humans and chimpanzees. The significance of Mojokerto's ECV relative to adult values is ambiguous, and Leigh (2006) pointed out that absolute, as opposed to relative, brain size (and, therefore, growth rates) provides important information about life history and cognition. If Mojokerto truly died around one year of age, the absolutely larger ECV would imply human-like levels of brain size growth during infancy (Leigh, 2006; Zollikofer and Ponce de León, 2013).

However, age estimates for Mojokerto range from early infancy to eight years. Estimates over six years are probably untenable because they are based on insufficient numbers of juvenile specimens (e.g., one–three, reviewed in Antón, 1997). Antón (1997) suggested an age of four to six years based on the closure of cranial fontanelles and sutures, and on glenoid fossa development compared with dentally-aged humans and Neandertals. Analyzing CT scans of the Mojokerto specimen, Coqueugniot et al. (2004) and Balzeau et al. (2005) discovered the individual's anterior fontanelle is patent, indicating both a younger age and further potential brain growth. Coqueugniot et al. (2004) assessed the ossification of two other cranial regions and found Mojokerto most likely died between the ages of 0.5–1.5 years based on both chimpanzee and human standards. Balzeau et al. (2005) analyzed the specimen's endocast and thought the impressions from the frontal lobe and a granular foveola suggested an older age, but probably no more than four years old. In sum, comparison with human and chimpanzee developmental series have suggested an age at death between early infancy and up to six years for Mojokerto, and the implications for brain growth in *H. erectus* depend entirely on its age. There is good reason to believe the individual died younger than two years of age based on recent assessments of metopic suture (Weinzweig et al., 2003; Bajwa et al., 2013) and anterior fontanelle closure in humans (Pindrik et al., 2014), but here we consider the full range of likely age estimates (up to six years) to highlight the importance of this uncertainty for interpreting brain growth in this species.

An important datum not included in earlier studies is neonatal brain size in *H. erectus*. DeSilva and Lesnik (2008) have shown that this value can be estimated (see also DeSilva, 2011) based on the high correlation between neonatal and adult brain size across anthropoids, including humans. Neonatal ECV estimates based on 20 *H. erectus* (*sensu lato*) adults range from 236.5 to 309.6 cm^3. With a range of neonatal ECVs and possible ages for the Mojokerto fossil, early postnatal growth rates in *H. erectus* can be examined in a comparative context.

Unlike previous work (e.g., Coqueugniot et al., 2004; O'Connell and DeSilva, 2013) our study examines absolute and proportional size change relative to calculated neonatal values (DeSilva and Lesnik, 2008). We compare postnatal brain growth in cross-sectional samples of humans ($n = 96$), *P. troglodytes* ($n = 58$), and *Gorilla beringei beringei* ($n = 20$), with that for ~1 Ma *H. erectus* using the range of potential ages of Mojokerto (Fig. 1). Randomly sampling pairs of neonates (≤0.03 years) and juveniles (>0.03 years) for each species, we calculate absolute and relative growth rates necessary to grow a neonatal brain to that at later ages. This pairwise resampling strategy incorporates uncertainty in both the range of neonatal brain size variation for *H. erectus* and the age at death of the Mojokerto specimen. This affords the statistical comparison of *H. erectus* with living species represented by larger samples and whose patterns of brain growth are better understood.

Materials and methods

ECVs for extant and fossil samples are from published sources (Table 1 and Supplementary Online Material [SOM] Dataset 1). Age at death is known for all individuals in the extant sample. In addition, the human (Coqueugniot and Hublin, 2012) and gorilla (McFarlin et al., 2013) samples are from single populations, thus reducing potential population effects. Chimpanzee data are from the Taï Forest (Neubauer et al., 2012) and the Yerkes National Primate Research Center (Herndon et al., 1999; DeSilva and Lesnik, 2006). Despite the different sources and brain size measurement (see below), the small Taï sample ($n = 9$) falls within the larger

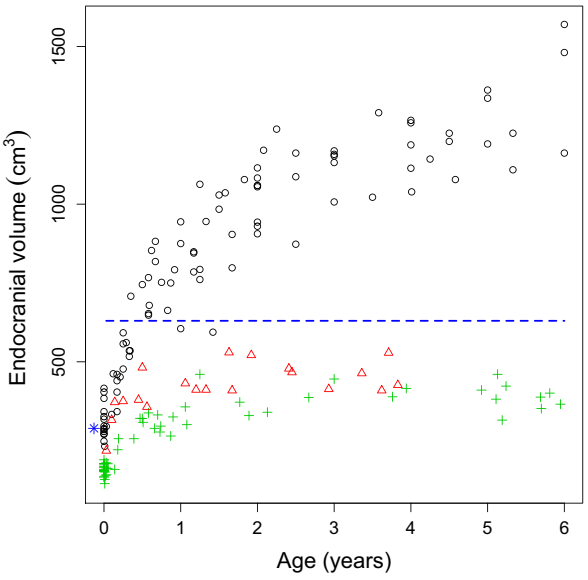

Figure 1. Empirical ECVs plotted against age. Humans are the black circles, chimpanzees the green crosses, and gorillas the red triangles. The Mojokerto ECV and estimated age range are indicated by the dashed blue line, and the estimated *H. erectus* neonatal mean ECV is the blue star. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Indonesian adult *H. erectus* sample and predicted neonatal ECVs.[a]

Specimen	ECV (cm^3)	Mojokerto PEV	Predicted neonate
Sangiran 4	908	0.69	287.1
Sangiran 2	813	0.77	265.0
Sangiran 10	855	0.74	274.9
Sangiran 12	1059	0.59	321.0
Sangiran 17	1004	0.63	308.8
Sangiran IX (Tjg-1993.05)	870	0.72	278.3
Bukaran (SBK-1996.02)	916	0.69	288.9
Grogol-Wetan (Gwn-1993.09)	850	0.74	273.7
Sangiran 3	950	0.66	296.7
Trinil	940	0.67	294.4
	Average	0.69	288.9

[a] Data are from O'Connell and DeSilva (2013) and sources therein. Neonatal ECV was estimated using the equation: log(neonatal brain) = 0.7246 × log(adult brain) + 0.3146 (DeSilva and Lesnik, 2008). Although this equation was specified for brain mass, the equation is unitless and so can be applied to volumes as well. PEV = percent adult endocranial volume.

Yerkes dataset (n = 49) for all ages considered. Although sex is known for nearly all individuals, we do not consider sex in our analysis as sex is unknown for the fossil sample and was not found to contribute significantly to ontogenetic variation in the chimpanzee (Neubauer et al., 2012) and human samples (Coqueugniot and Hublin, 2012).

Captive chimpanzee (Herndon et al., 1999) and wild gorilla (McFarlin et al., 2013) ECVs were estimated from masses using equations provided in Smith et al. (1995:157): ECV = (brain mass) *1.05 (Jerison, 1973), and ECV = 0.94*(brain mass)$^{1.02}$ (Martin, 1990). It is not clear which equation is most appropriate, so for each brain mass we use the average estimated from both equations. Predictions are very similar between equations and our analysis results do not differ depending on which is used.

We use Balzeau et al.'s (2005) CT-based volume estimate of 630 cm^3 for Mojokerto, and although it is slightly lower than Coqueugniot et al.'s (2004) estimate of 663 cm^3, results do not differ depending on which estimate is used. *H. erectus* neonatal ECV is estimated at 288.9 cm^3, based on ≥1 Ma Indonesian adult ECVs using an equation for estimating catarrhine neonatal ECV (see Table 1; DeSilva and Lesnik, 2008). We include only Indonesian *H. erectus* since these have close temporal and presumed phylogenetic affinity with Mojokerto (e.g., Antón, 1997). This adult sample leads to a higher neonatal ECV estimate than the full *H. erectus s. l.* hypodigm (DeSilva and Lesnik, 2008), conservatively biasing against higher growth rates.

We simulate variation around this estimated mean by drawing from a hypothetical normal distribution of *H. erectus* neonates in R (R Core Team, 2012). The creation of a normal distribution requires specifying both a mean and standard deviation (SD). While there are biological grounds for specifying a mean (DeSilva and Lesnik, 2006, 2008), the selection of standard deviation is more arbitrary. Applying the coefficients of variation (CV) of the human (SD = 55 cm^3, CV = 0.18) and chimpanzee (SD = 19 cm^3, CV = 0.12) neonatal samples to our estimated *H. erectus* mean results in SDs of 51.2 and 34.5 cm^3, respectively. The larger, human-like SD produces unreasonable neonatal values from 93 to 478 cm^3 (95% quantiles = 188–390 cm^3). The full range extends beyond both chimpanzee and human extremes, and the 95% quantiles overlap the largest chimpanzee and 13/15 human neonates. Neonates simulated using the chimpanzee-based SD, on the other hand, range from 150 to 404 cm^3, with 95% quantiles (222–356 cm^3) above chimpanzees but subsuming the lower half of the human distribution. The simulation using the smaller SD therefore probably produces the most realistic results and so is the parameter used in simulations.

We acknowledge that incomplete preservation creates inherent error in the estimate of fossil ECV. This error will be greater for some fossils than for others due to both preservation and the methods used to estimate volume. We cannot account for this error in the estimation of neonatal ECV. However, our simulation does include a range of variation about a mean neonatal value, which may at least partially make up for error in estimation of adult ECV.

We consider neonates to be ≤0.03 years, as this is the age of the youngest gorilla in our extant sample and was used as the neonate-infant cutoff in previous analyses (DeSilva and Lesnik, 2006, 2008). ECVs of individuals older than this age fall outside the range of variation for both human and chimpanzee neonates (age = 0). Because Mojokerto is likely no older than six years (Antón, 1997; Coqueugniot et al., 2004; Balzeau et al., 2005), we only include extant samples up to age six. Chronological age at death is known for extant samples. As detailed below, age at death for Mojokerto is allowed to vary between infancy (>0.03 years) and six years.

To use resampling to compare ECV growth between extant taxa and *H. erectus*, our analysis asks what proportion and magnitude of size change are necessary to 'grow' an empirical or predicted neonatal brain size to that of an older individual. This approach is useful for examining small fossil samples for which growth or velocity curves cannot be reliably reconstructed. We calculate proportional size changes (PSCs) and absolute average annual rates (ARs) from resampled pairs including neonates and older individuals. Resampling is done using custom algorithms in R (R Core Team, 2012), which are freely available upon request. The procedure for extant taxa is as follows:

1. Randomly select a neonate and a juvenile, recording their brain sizes and the juvenile's age in years (neonatal age is assumed to be 0 for simplicity). Note that there is only one gorilla neonate.
2. Repeat 5000 times, and omit all resulting non-unique pairwise comparisons, as well as those implying brain size reduction.
3. Use these vectors to calculate both the AR and PSC implied by a resampled pair's brain sizes:
   a. PSC = juvenile ECV/neonate ECV. This is the factor by which brain size increases from birth to a given age, and is not a rate of change.
   b. AR = (juvenile ECV-neonate ECV)/juvenile age. This is the implied rate of average size change in cm^3 per year, for a given age.

The following algorithm is used for *H. erectus*:

1. Randomly select a neonatal ECV estimate from a normal distribution (mean = 288.9, SD = 34.5) using R's rnorm() function.
2. Randomly select an age for Mojokerto, from a concatenated vector of the empirical extant non-neonatal ages (between 0.05 and 6.0 years).
3. Repeat 5000 times, resulting in two vectors of resampled variables. PSC and AR are calculated as above, using a juvenile ECV vector of length 5000 whose entries are only the Mojokerto child's ECV.

Resampled PSCs and ARs are analyzed with the standard statistics package in R.

Results

Extant taxa

Results of resampling neonatal + juvenile pairs of ECVs for both relative and absolute size change (PSCs and ARs, respectively; SOM Dataset 2) are consistent with previous studies of brain growth in

humans and African apes (Vrba, 1998; Leigh, 2004; McFarlin et al., 2013). There is extensive overlap between species' PSCs in the first postnatal year (cf. Zollikofer and Ponce de León, 2013: Fig. B5), although human values (solid line) are generally elevated above those of apes (dashed and dotted lines in Fig. 2). Gorilla PSCs plateau after two years (median = 2.13), and chimpanzee PSCs plateau after three years (median = 2.53). In contrast, human PSCs continue increasing up to six years.

Some chimpanzee (23/803) and human (8/1178) resampled ARs are below 0 cm^3/yr, due to slight overlap between neonatal and infant ECVs. Negative ARs are unrealistic as they imply brain size reduction, and so these values are omitted from subsequent analysis. Human and chimpanzee ARs show a similar, highly variable, pattern for the first 0.30 years, due to cross-sectional samples (solid and dashed lines, respectively, in Fig. 3); the gorilla sample is not large enough to produce such variation and overlap. Gorilla ARs are in the human range up to 0.25 years. All extant species show rapid decline from birth to around 0.50 years, and then more gradual decline after the first year. Apes overlap the lower half of the human range prior to 0.50 years, but thereafter fall below the human distribution. ARs begin to level off after around two years in apes but not until around four in humans. Note that ARs represent the average amount of size increase per year to a given age, and so this plateau does not necessary indicate the cessation of brain size growth.

Homo erectus

There is, essentially, an identical distribution of *H. erectus* PSCs across ages (Fig. 2) because we sampled from the same neonatal ECV distribution for all ages. The median *H. erectus* PSC (2.17, 95% quantiles = 1.77–2.82) approximates the empirical ratio of Mojokerto to the estimated neonatal mean (2.18). The 95% quantiles (upper and lower blue lines in Fig. 2) encompass most of the human range from 0.35 to 1.33 years. Thereafter, only the upper half of the *H. erectus* range encompasses only the lower part of the human range. The *H. erectus* 95% quantiles enter the chimpanzee range (dashed lines in Fig. 2) at 0.18 years, and by three years the lower two thirds of the chimpanzee range fall within the upper half of the *H. erectus* distribution. Gorilla PSCs (triangles in Fig. 2) are below the *H. erectus* 95% quantiles until 0.5 years, and by 1.67 years the gorilla distribution straddles the *H. erectus* median.

Fig. 3 shows the resampled ARs plotted against age. All simulated *H. erectus* ARs prior to 0.35 years are higher than the extant maxima. We consider such extreme values for *H. erectus* unlikely, and so these (n = 378/5000) are not figured or considered further. Between 0.35 and 1.0 years, *H. erectus* ARs (median = 532 cm^3/yr) fall within the lower end of the human range (median = 631 cm^3/yr). After 1.33 years there is little overlap of the human and *H. erectus* ranges (the overlap at 1.42 years is due to a single human outlier), and distributions are completely separate after 2.50 years.

Importantly, *H. erectus* ARs always exceed those of apes, with no overlap in quantiles except at 1.25 years, which is due to a single, adult-sized chimpanzee. After one year, *H. erectus* ARs (median = 132 cm^3/yr) are significantly higher than chimpanzees' (median = 62 cm^3/yr) based on a Wilcoxon rank-sums test ($W = 299{,}548$, $p = 2.2 \times 10^{-16}$) and are higher than gorillas' (median = 108), but not significantly so ($W = 16{,}275$, $p = 0.16$). In summary, the average rate of ECV growth implied by Mojokerto is largely within the human range between 0.35 and 1.17 years, and rates implied by older ages fall between empirical human and ape ranges.

Discussion

The resampling strategy used here allows inference of early postnatal ECV growth in *H. erectus* in the light of uncertainties

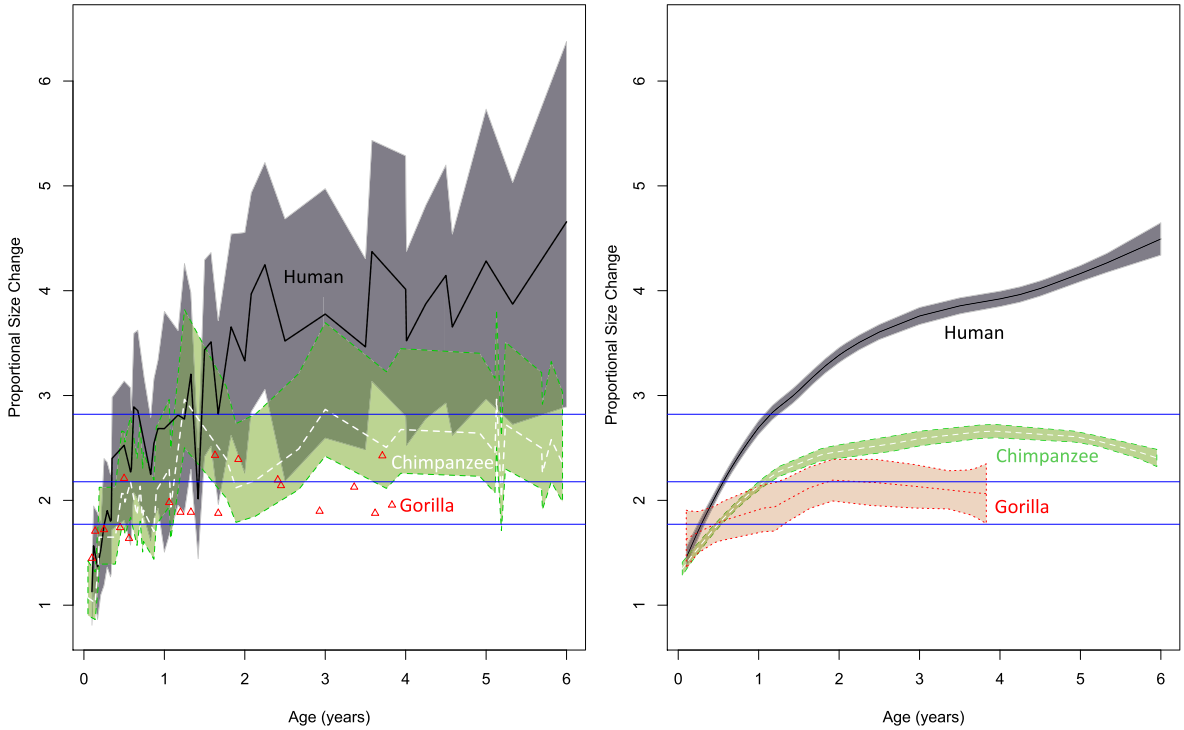

Figure 2. PSC plotted against age. Colors are as in Fig. 1. Left: For humans (black/gray) and chimpanzees (green/white), species medians are represented by heavy black (human) and white (chimpanzee) lines, and the shaded areas encompass the 95% quantiles. The thin horizontal blue lines encompass the *H. erectus* 95% quantiles and the heavy blue line marks the median. The actual gorilla PSC points are plotted. Right: Loess regression lines for extant species with 95% confidence intervals shaded. The left plot highlights the complexity inherent to cross-sectional samples, while the right plot highlights their smoothed, inferred central tendencies. Note that the range of overlap between species is clear in the left plot but not apparent in the smoothed right plot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

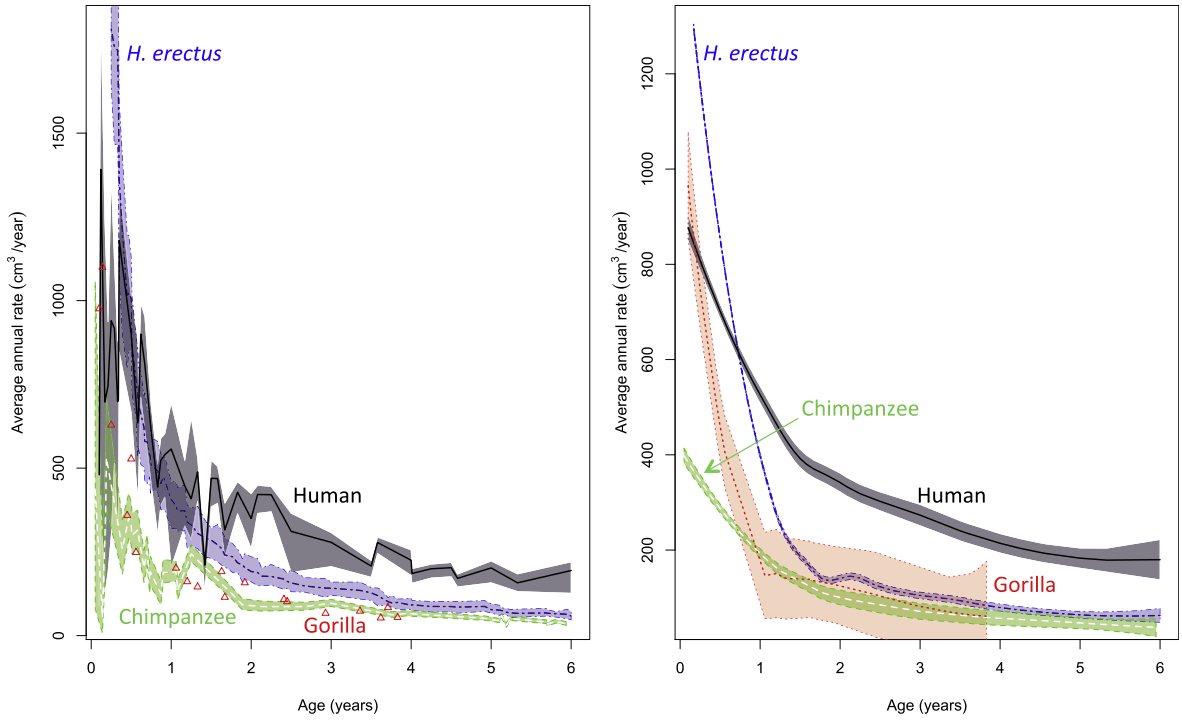

Figure 3. AR plotted against age; colors as in Fig. 2. Left: Human, chimpanzee, and *H. erectus* resampled AR medians (heavy lines) and 95% quantiles (shaded). Gorilla ARs are represented by actual points. Right: Loess regression lines for all taxa with 95% confidence intervals shaded. Note the contrasting inferences afforded by the raw (left) and smoothed (right) data plots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

about neonatal ECV and the age at death of the only juvenile *H. erectus* specimen with a reliable ECV estimate. This approach is useful for getting the most out of a very limited fossil record and can be applied to different datasets and research questions. Although individual variation (e.g., due to sex or idiosyncrasy) increases inferred variability in cross-sectional samples, fossil samples are cross-sectional by definition. Our resampling approach, calculating absolute and proportional size changes from pairs of extant specimens, provides a statistical basis for interpreting simulated *H. erectus* values and deeming brain growth ape- or human-like (if either). Resampling and simulation highlight central tendencies (e.g., PSC at a given age) and demonstrate the range of variation that can be observed in cross-sectional samples.

Parameters for simulating *H. erectus* PSCs and ARs are defined largely by the fossil record itself. Although no *H. erectus* neonatal ECVs are empirically known, likely values can be estimated from adult ECV (DeSilva and Lesnik, 2008). Indeed, the equation we used to predict average *H. erectus* neonatal ECV correctly estimates neonatal ECV for Neandertals (DeSilva, 2011), for which there are two fossil neonates whose cranial vaults and ECVs can be reconstructed (Ponce de León et al., 2008; Gunz et al., 2011, 2012). Neonatal ECV estimation is dependent upon the adult values used in the prediction equation, and therefore specific subsets of *H. erectus* adults or the entire species hypodigm will yield different estimates of neonatal ECV (DeSilva and Lesnik, 2008). We assumed Early Pleistocene Indonesian *H. erectus* adults were an appropriate sample for two reasons. First, they are temporally and geographically similar, albeit not identical, to the Mojokerto fossil (Huffman et al., 2006), and these presumably have the closest population affinity with the specimen. Second, this sample has a higher average ECV than the greater Early Pleistocene *H. erectus* hypodigm and therefore yields a relatively high estimate of neonatal ECV. Simulated PSCs and ARs are therefore lower than would be estimated from smaller adult ECVs, and are thus the most conservative approach.

Our estimated *H. erectus* neonatal ECV, at 288.9 cm^3, is slightly below the 315 cm^3 estimated maximum neonatal head size inferred from the BSN49/P27 pelvis from Gona, Ethiopia (Simpson et al., 2008). Assuming this small but capacious pelvis represents an accurate upper limit for contemporaneous Indonesian *H. erectus*, this limit removes higher neonatal ECVs and therefore slightly lower PSCs and ARs. Simulated PSCs based on *H. erectus* neonates no greater than this maximum (n = 3892/5000) range from 2.00 to 4.04 (median = 2.26). ARs (omitting unrealistically high values) calculated from neonatal ECVs below this limit (n = 3584, median = 202.5 cm^3/yr) are slightly higher than in the full simulated dataset (median = 193.9 cm^3/yr).

The most significant determinant of which simulated PSCs and ARs are most realistic is the chronological age of Mojokerto itself. Simulated absolute growth rates are within the human range if the specimen was around one year, but intermediate between humans and apes at older ages. Although Antón (1997) favored an age from four to six years, we consider a younger age likely for several reasons. First and foremost is the specimen's open anterior fontanelle, which a recent CT-based study (Pindrik et al., 2014) found to be fully closed by 2.5 years in 90% of 459 healthy humans, though fusion frequency exceeded 50% by 16 months. Second, Coqueugniot et al. (2004) found the highest likelihood of observing humans with anterior fontanelle and subarcuate fossa closure comparable to Mojokerto between the ages of 0.5–1.5 years. Fontanelle and subarcuate fontanelle closure occurred by three months in their chimpanzee sample. These authors found tympanic plate fusion, one of Antón's (1997) bases for an older age, to be unreliable as it could be found fully closed in humans and apes of all ages. Along these lines, ontogenetic variation in other features possibly indicative of an older age for Mojokerto (e.g., glenoid fossa: Antón, 1997; digital impressions and granular foveolae: Balzeau et al., 2005)

must be analyzed further to assess their usefulness as age indicators. Third, most assessments of Mojokerto's age have been based on human standards, but dental evidence suggests *H. erectus* may have attained developmental milestones at younger ages than recent humans (Dean et al., 2001; Dean and Smith, 2009). Human standards therefore may overestimate Mojokerto's age. In conclusion, Mojokerto's open anterior fontanelle, coupled with dental evidence for accelerated development in *H. erectus* compared with humans, suggest an upper age limit younger than 2.5 years, if not closer to one year.

The fully fused metopic suture of Mojokerto (Antón, 1997; Coqueugniot et al., 2004; Balzeau et al., 2005) potentially provides a minimum age at death of eight months. Full fusion of the metopic suture occurs around eight months (Weinzweig et al., 2003), but not later than 15 months (Bajwa et al., 2013) in modern humans. Falk et al. (2012) found a much higher incidence of un- or incompletely fused metopic sutures at later ages, but they nevertheless found metopic suture had occurred by dm_2 eruption in the majority of human (50%) and *P. troglodytes* (80%) specimens. In sum, the chronology of metopic suture and anterior fontanelle closure is well known in chimpanzees and humans, and along with dental evidence for advanced dental maturation compared with humans, suggest Mojokerto died between 0.67 and 2.0 years, and we therefore consider an age at death around one year quite reasonable (cf. Coqueugniot et al., 2004).

PSCs and ARs obtained here are also consistent with this range for Mojokerto's age at death. Simulated *H. erectus* ARs prior to 0.35 years are higher than in all extant species, making such values improbable. *H. erectus* PSCs encompass most of the empirical extant taxa's ranges by six months. But, the *H. erectus* distribution generally falls below the (phylogenetically close) human and chimpanzee distributions by around 2.5 years. Therefore, based on brain growth patterns alone, Mojokerto is likely to be between 0.35 and 2.5 years old, independently supporting the age range proposed by Coqueugniot et al. (2004) based on preserved anatomy.

If the Mojokerto individual died between 1.5 and 2.5 years, our results imply absolute brain size growth rates intermediate between humans and apes. However, if the individual died between 0.5 and 1.5 years as Coqueugniot et al. (2004) have suggested, brain growth rates in *H. erectus* infants would have been in the lower half of the modern human range (cf. Leigh, 2006; Zollikofer and Ponce de León, 2013), supporting previous claims for secondary altriciality in this species (Martin, 1983; Walker and Ruff, 1993). In humans, brain expansion during the first two years of life is driven by the proliferation of white matter and neural connectivity (Sakai et al., 2013). If *H. erectus* infants also experienced rapid brain growth driven by white matter proliferation, this may also imply some level of similarity in cognitive (e.g., social) development as well.

Given the exceptionally high energetic demands of brain tissue (Holliday, 1986; Leonard et al., 2003; Kuzawa et al., 2014), and the high likelihood that *H. erectus* infants were nursed throughout at least the first year of their lives (Austin et al., 2013), the challenge of meeting these elevated energetic needs of the growing infant would have rested on *H. erectus* females. How *H. erectus* met these energetic challenges is unclear, although there is a suite of anatomical, behavioral, and technological changes associated with early *H. erectus* that would have increased their available energy budgets (Pontzer, 2012). There is evidence that early *Homo* experienced a transition to higher quality food items (Leonard and Robertson, 1996; Aiello and Key, 2002), including more meat and aquatic resources. The latter appear to have been especially important in Java, with faunal signatures of diverse fresh- and saltwater exploitation at Trinil (Joordens et al., 2009). This increase in dietary breadth and quality did not necessarily require advanced lithic technology, which is notably absent in the Indonesian record where other materials such as shells and shark teeth appear to have been used instead (Joordens et al., 2015). Cooking technologies may have also been important in expanding the dietary breadth necessary to fuel the fast-growing brain in *H. erectus* (Wrangham, 2009).

It has been suggested that cooperative breeding and perhaps shared parental care (Hrdy, 2009; Isler and van Schaik, 2012) by early *Homo* increased food sharing opportunities and helped mitigate the energetic burden on females. Isler and Van Schaik (2009, 2012, 2014) have argued that without alloparental care, large-brained hominin infants could not be produced fast enough to maintain population stability. Indeed, alloparenting may have also evolved alongside increased brain size in social carnivores as well (Smith et al., 2012), suggesting shared responsibility for offspring is a viable if not common strategy to break the energetic restraint of growing large brains. Results presented here provide a proximate mechanism for increased brain size in *H. erectus*, and this energetically costly strategy probably could not have evolved without both increased energy turnover and cooperative breeding and foraging.

In sum, we consider it likely that the Mojokerto individual died under 2.5 years of age, and probably close to one year, implying *H. erectus* experienced absolute rates of brain growth at the lower end of the observed human range. Even if this individual is older, our results indicate that absolute brain growth rates in this species would have been lower than in humans but higher than in apes. If the lower age range is correct, some of the key alterations in human brain ontogeny, and the behavioral and cultural changes required to sustain the accompanying energetic demands, had evolved by at least one million years ago.

Acknowledgments

We are grateful to the numerous authors who published their endocranial volume and brain mass data for extant and fossil specimens. S. McFarlin aided in gathering information about *G. beringei* data. D.L. Begun provided useful comments and suggestions in the early stages of this work. Comments and suggestions from Peter Ellison, Sarah Elton, the Associate Editor and anonymous reviewers further helped improve the quality of this study and manuscript drafts.

Appendix A. Supplementary data

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.jhevol.2015.02.011.

References

Aiello, L.C., Wheeler, P., 1995. The Expensive-Tissue Hypothesis: the brain and the digestive system in human and primate evolution. Curr. Anthropol. 36, 199–221.
Aiello, L.C., Key, C., 2002. Energetic consequences of being a *Homo erectus* female. Am. J. Hum. Biol. 14, 551–565.
Antón, S.C., 1997. Developmental age and taxonomic affinity of the Mojokerto child, Java, Indonesia. Am. J. Phys. Anthropol. 102, 497–514.
Austin, C., Smith, T.M., Bradman, A., Hinde, K., Joannes-Boyau, R., Bishop, D., Hare, D.J., Doble, P., Eskenazi, B., Arora, M., 2013. Barium distributions in teeth reveal early-life dietary transitions in primates. Nature 498, 216–220.
Bajwa, M., Srinivasan, D., Nishikawa, H., Rodrigues, D., Solanki, G., White, N., 2013. Normal fusion of the metopic suture. J. Craniofac. Surg. 24, 1201–1205.
Balzeau, A., Grimaud-Hervé, D., Jacob, T., 2005. Internal cranial features of the Mojokerto child fossil (East Java, Indonesia). J. Hum. Evol. 48, 535–553.
Coqueugniot, H., Hublin, J.-J., 2012. Age-related changes of digital endocranial volume during human ontogeny: results from an osteological reference collection. Am. J. Phys. Anthropol. 147, 312–318.
Coqueugniot, H., Hublin, J.-J., Veillon, F., Houët, 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 New York Acad. Sci. 46, 993–1122.
Dean, M.C., Leakey, M.G., Reid, D., Schrenk, F., Schwartz, G.T., Stringer, C., Walker, A., 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414, 628–631.
Dean, M.C., Smith, B.H., 2009. Growth and development of the Nariokotome Youth, KNM-WT 15000. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), The First Humans: Origin and Early Evolution of the Genus *Homo*. Springer, New York, pp. 101–120.
DeSilva, J.M., 2011. A shift toward birthing relatively large infants early in human evolution. Proc. Natl. Acad. Sci. 108, 1022–1027.
DeSilva, J.M., Lesnik, J.J., 2006. Chimpanzee neonatal brain size: implications for brain growth in *Homo erectus*. J. Hum. Evol. 51, 207–212.
DeSilva, J.M., Lesnik, J.J., 2008. Brain size at birth throughout human evolution: a new method for estimating neonatal brain size in hominins. J. Hum. Evol. 55, 1064–1074.
Dobbing, J., Sands, J., 1979. Comparative aspects of the brain growth spurt. Early Hum. Dev. 311, 79–83.
Dunsworth, H.M., Warrener, A.G., Deacon, T., Ellison, P.T., Pontzer, H., 2012. Metabolic hypothesis for human altriciality. Proc. Natl. Acad. Sci. 109, 15212–15216.
Falk, D., Zollikofer, C.P.E., Morimoto, N., Ponce de León, M.S., 2012. Metopic suture of Taung (*Australopithecus africanus*) and its implications for hominin brain evolution. Proc. Natl. Acad. Sci. 109, 8467–8470.
Gunz, P., Neubauer, S., Maureille, B., Hublin, J.-J., 2011. Virtual reconstruction of the Le Moustier 2 newborn skull. Implications for Neandertal ontogeny. Paleo 22, 155–172.
Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., Hublin, J.-J., 2012. A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. J. Hum. Evol. 62, 300–313.
Herndon, J.G., Tigges, J., Anderson, D.C., Klumpp, S., McClure, H.M., 1999. Brain weight throughout the life span of the chimpanzee. J. Comp. Neurol. 409, 567–572.
Hofman, M.A., Falk, D. (Eds.), 2012. Evolution of the Primate Brain. Elsevier, New York.
Holliday, M.A., 1986. Body composition and energy needs during growth. In: Falkner, F., Tanner, J.M. (Eds.), Human Growth: A Comprehensive Treatise. Plenum Press, New York, pp. 101–117.
Hrdy, S., 2009. Mothers and Others: The Evolutionary Origins of Mutual Understanding. Belknap Press, Cambridge.
Huffman, O.F., Zaim, Y., Kappelman, J., Ruez, D.R.J., de Vos, J., Rizal, Y., Aziz, F., Hertler, C., 2006. Relocation of the 1936 Mojokerto skull discovery site near Perning, East Java. J. Hum. Evol. 50, 431–451.
Isler, K., van Schaik, C.P., 2009. The expensive brain: a framework for exploring evolutionary changes in brain size. J. Hum. Evol. 57, 392–400.
Isler, K., van Schaik, C.P., 2012. How our ancestors broke through the gray ceiling: comparative evidence for cooperative breeding in early *Homo*. Curr. Anthropol. 53, S453–S465.
Isler, K., van Schaik, C.P., 2014. How humans evolved large brains: comparative evidence. Evol. Anthropol. 23, 65–75.
Jerison, H.J., 1973. Evolution of the Brain and Intelligence. Academic Press, New York.
Joordens, J.C.A., Wesselingh, F.P., de Vos, J., Vonhof, H.B., Kroon, D., 2009. Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia). J. Hum. Evol. 57, 656–671.
Joordens, J.C.A., d'Errico, F., Wesselingh, F.P., Munro, S., de Vos, J., Wallinga, J., Ankjærgaard, C., Reimann, T., Wijbrans, J.R., Kuiper, K.F., Mücher, H., Coqueugniot, H., Prié, V., Joosten, I., van Os, B., Schulp, A.S., Panuel, M., van der Haas, V., Lustenhouwer, W., Reijmer, J.J.G., Roebroeks, W., 2015. *Homo erectus* at Trinil on Java used shells for tool production and engraving. Nature 518, 228–231.
Kuzawa, C.W., Chugani, H.T., Grossman, L.I., Lipovich, L., Muzik, O., Hof, P.R., Wildman, D.E., Sherwood, C.C., Leonard, W.R., Lange, N., 2014. Metabolic costs and evolutionary implications of human brain development. Proc. Natl. Acad. Sci. 111, 13010–13015.
Leigh, S.R., 2004. Brain growth, life history, and cognition in primate and human evolution. Am. J. Primatol. 164, 139–164.
Leigh, S.R., 2006. Brain ontogeny and life history in *Homo erectus*. J. Hum. Evol. 50, 104–108.
Leonard, W.R., Robertson, M.L., 1996. On diet, energy metabolism, and brain size in human evolution. Curr. Anthropol. 37, 125–129.
Leonard, W.R., Robertson, M.L., Snodgrass, J., Kuzawa, C.W., 2003. Metabolic correlates of hominid brain evolution. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. 136, 5–15.
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: Fifty-Second James Arthur Lecture on the Evolution of the Human Brain. American Museum of Natural History, New York.
Martin, R.D., 1990. Primate Origins and Evolution. A Phylogenetic Reconstruction. Princeton University Press, Princeton.
McFarlin, S.C., Barks, S.K., Tocheri, M.W., Massey, J.S., Eriksen, A.B., Fawcett, K.A., Stoinski, T.S., Hof, P.R., Bromage, T.G., Mudakikwa, A., Cranfield, M.R., Sherwood, C.C., 2013. Early brain growth cessation in wild Virunga mountain gorillas (*Gorilla beringei beringei*). Am. J. Primatol. 75, 450–463.
Montagu, A., 1971. Touching: The Human Significance of the Skin. William Morrow Paperbacks, New York.
Neubauer, S., Gunz, P., Schwarz, U., Hublin, J.-J., Boesch, C., 2012. Endocranial volumes in an ontogenetic sample of chimpanzees from the Taï Forest National Park, Ivory Coast. Am. J. Phys. Anthropol. 147, 319–325.
O'Connell, C.A., DeSilva, J.M., 2013. Mojokerto revisited: evidence for an intermediate pattern of brain growth in *Homo erectus*. J. Hum. Evol. 65, 156–161.
Pindrik, J., Ye, X., Ji, B.G., Pendleton, C., Ahn, E.S., 2014. Anterior fontanelle closure and size in full-term children based on head computed tomography. Clin. Pediatr. 53, 1149–1157.
Ponce de León, M.S., Golovanova, L., Doronichev, V., Romanova, G., Akazawa, T., Kondo, O., Ishida, H., Zollikofer, C.P.E., 2008. Neandertal brain size at birth provides insights into the evolution of human life history. Proc. Natl. Acad. Sci. 105, 13764–13768.
Pontzer, H., 2012. Ecological energetics in early *Homo*. Curr. Anthropol. 53, S346–S358.
Portmann, A., 1941. Die Tragzeiten der Primaten und die Dauer der Schwangerschaft beim Menschen: Ein Problem der vergleichenden Biologie. Rev Suisse Zool 48, 511–518.
R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL. http://www.R-project.org/.
Roelfsema, N., Hop, W., Boito, S., Wladimiroff, J., 2004. Three-dimensional sonographic measurement of normal fetal brain volume during the second half of pregnancy. Am. J. Obstet. Gynecol. 190, 275–280.
Sakai, T., Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., Makishima, H., Eguchi, T., Yamada, S., Ogihara, N., Takeshita, H., 2012. Fetal brain development in chimpanzees versus humans. Curr. Biol. 22, R791–R792.
Sakai, T., Matsui, M., Mikami, A., Malkova, L., Hamada, Y., Tomonaga, M., Suzuki, J., Tanaka, M., Miyabe-Nishiwaki, T., Makishima, H., Nakatsukasa, M., Matsuzawa, T., 2013. Developmental patterns of chimpanzee cerebral tissues provide important clues for understanding the remarkable enlargement of the human brain. Proc. R. Soc. B 280, 20122398.
Simpson, S.W., Quade, J., Levin, N.E., Butler, R., Dupont-Nivet, G., Everett, M., Semaw, S., 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. Science 322, 1089–1092.
Smith, J.E., Swanson, E.M., Reed, D., Holekamp, K.E., 2012. Evolution of cooperation among mammalian carnivores and its relevance to hominin evolution. Curr. Anthropol. 53, S436–S452.
Smith, R.J., Gannon, P.J., Smith, B.H., 1995. Ontogeny of australopithecines and early *Homo*: evidence from cranial capacity and dental eruption. J. Hum. Evol. 29, 155–168.
Vrba, E.S., 1998. Multiphasic growth models and the evolution of prolonged growth exemplified by human brain evolution. J. Theor. Biol. 190, 227–239.
Walker, A., Ruff, C.B., 1993. The reconstruction of the pelvis. In: Walker, A., Leakey, R.E. (Eds.), The Nariokotome *Homo erectus* skeleton. Harvard University Press, Cambridge, pp. 221–233.
Weinzweig, J., Kirschner, R.E., Farley, A., Reiss, P., Hunter, J., Whitaker, L.A., Bartlett, S.P., 2003. Metopic synostosis: defining the temporal sequence of normal suture fusion and differentiating it from synostosis on the basis of computed tomography images. Plast. Reconstr. Surg. 112, 1211–1218.
Wrangham, R., 2009. Catching Fire: How Cooking Made Us Human. Basic Books, New York.
Zollikofer, C.P.E., Ponce de León, M.S.P., 2013. Pandora's growing box: inferring the evolution and development of hominin brains from endocasts. Evol. Anthropol. 22, 20–33.