A neonatal perspective on *Homo erectus* brain growth

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**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.

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**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.
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 exothergestation (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 most important correlates of life history and material 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 cm³. 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 Tai 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 Tai sample (n = 9) falls within the larger
Applying the coefficient $\frac{1}{n}$ (SD specifying both a mean and standard deviation (SD). While there are statistics package in R. The creation of a normal distribution requires biasing against higher growth rates.

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 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 $\geq 1$ 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. I. 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 $\leq 0.03$ 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 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:

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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

Table 1
Indonesian adult H. erectus sample and predicted neonatal ECVs.\(^a\)

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

\(^a\) 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.
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 cm³/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 necessarily 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 cm³/yr) fall within the lower end of the human range (median = 631 cm³/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 quantities except at 1.25 years, which is due to a single, adult-sized chimpanzee. After one year, *H. erectus* ARs (median = 132 cm³/yr) are significantly higher than chimpanzees’ (median = 62 cm³/yr) based on a Wilcoxon rank-sums test (W = 299,548, p = 2.2 × 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...
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 (Weinzeig 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, suggests 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.

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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


