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Journal of Human Evolution 50 (2006) 109–113
JHE

News and Views

Absolute or proportional brain size: That is the question. A reply to Leigh's (2006) comments

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Received 21 March 2005; accepted 25 August 2005

Keywords: Brain growth; Brain evolution; Cognition

In his comments, Leigh (2006) argues that when absolute brain size rather than proportional size is plotted against age, the juvenile *Homo erectus* specimen Mojokerto falls into the extant *Homo sapiens* range of variation. On the other hand, we showed that, when proportional endocranial volume (PEV, i.e., the ratio between the endocranial volume of an individual at a given age and the average adult endocranial volume) is used as the means of comparison, Mojokerto falls within the chimpanzee range rather than the human range (Coqueugniot et al., 2004). Although these observations may seem contradictory, there is, in fact, no major disagreement between them. Absolute and proportional brain sizes address different questions. Additionally, that *H. erectus* and *H. sapiens* may have had similar absolute brain sizes at an early age does not necessarily imply similar developmental curves. As the adult brain size is quite different between the two species, this may actually imply different developmental trajectories. Finally, with respect to the variability of absolute and proportional brain size in humans and apes, our data yield different results than do the data used by Leigh. This discrepancy may result from several methodological issues that we also find important to clarify.

Age determination for Mojokerto

It is certainly possible to debate our age determination for Mojokerto of 0.5–1.5 years. However, previous age estimates (from one to eight years old) have been based on vague arguments, including some based on the braincase size of the specimen, which led to circular reasoning about brain development. We utilized the most accurate available age indicators. The *fossa subarcuata* closure and the fontanelle were most reliable. Our study also showed that the external tympanic morphology, mentioned by Leigh, is a poor age indicator. A fused or unfused state of the tympanic plate is observed at variable frequencies in all the age classes between birth and adulthood. It should be noted that, if, based on this feature, an older individual age (ca. 4–6 years old) is favored for Mojokerto, then the PEV of this juvenile *H. erectus* would be closer to the modern human distribution (Fig. 1), but its absolute brain size would be pushed farther away from the modern human distribution.

Problems with material and methodology

The study of brain development in fossil hominins is primarily based on measurement of the endocranial volume (EV). In contrast, the data utilized by Leigh represent post-autopsy brain weights, whereby EV is estimated by applying a coefficient of specific gravity. The autopsy data introduce important limitations for precisely inferring EV and for evaluating its variability in humans and in apes. The cerebrospinal fluid surrounding the brain represents about 12% of the endocranial cavity (Peters et al., 1998). During an autopsy, a variable quantity of the cerebrospinal fluid escapes from the subarachnoid space and from the ventricles, making it difficult to accurately control for this factor a posteriori. Another important factor that artificially increases variability is the cause

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doi:10.1016/j.jhevol.2005.08.009

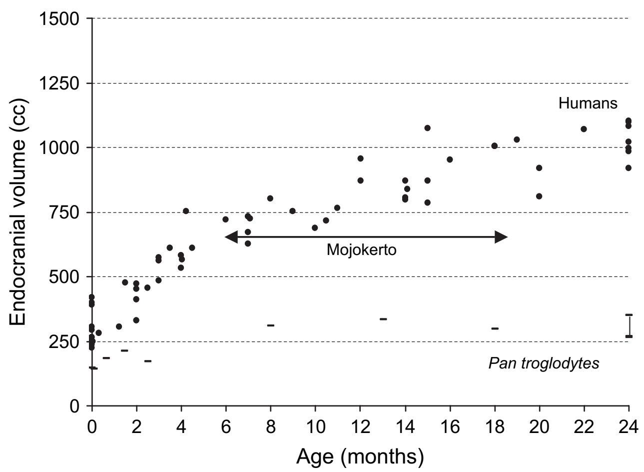

Fig. 1. Endocranial volume of Mojokerto (represented by an arrow) compared to the endocranial volume of the Strasbourg human immature series and the *Pan troglodytes* juvenile series from the Museum National d'Histoire Naturelle (Paris) (for sample compositions, see Coqueugniot et al., 2004). Endocranial volume (on the y-axis) is plotted against calendar age (x-axis).

of death. In particular, it is common knowledge in neuropathology that a number of causes of death result in brain edemas and the brain weight is, by itself, an element of diagnosis in the autopsy room. The human weight series used by Leigh was collected in the late nineteenth century by Marchand (1902). Marchand listed a number of pathologies (especially infectious diseases) and different causes of death that directly interact with the actual size of the brain to influence the brain weight, especially in autopsied children. Interestingly (and especially important for the issues discussed here), he concluded that the only way to solve this problem would be to measure the exact endocranial volumes of subjects rather than their weights (Marchand, 1902: 398, 408). Marchand emphasized the need to exclude extreme weight values. Accordingly, we find it difficult to assess the intraspecific variability and overlap between species in EV when it is estimated from brain weight from such series. Similar problems apply to chimpanzee data which, in addition, are characterized by a very high rate of premature birth—of the neonates necropsied at Yerkes, 29% died of "prematurity/anoxia" (McClure et al., 1994). One may argue that Mojokerto also died at an early age and perhaps from an infectious disease; however this certainly did not artificially increase this individual's EV. In our study of modern children (Coqueugniot et al., 2004), EV was directly measured in a relatively large sample of individuals of known age, under conditions comparable to those under which measurements for the fossil skulls were performed. Following this approach, the observed variation and overlap between species are less spectacular than in the studies based on brain weights (Fig. 1).

Absolute brain size and overlap between *H. sapiens* and *H. erectus* neonates

We agree with Leigh that absolute brain size at birth and soon after is important, especially in terms of physiological costs and obstetrical constraints. Martin (1983) established that brain size at birth (E_N) among primates is strongly related to body mass at birth (P_N). The two variables are related by an allometric equation: $\mathrm{Log}_{10}(E_N) = 0.96 \times \mathrm{Log}_{10}(P_N) + 2.12$. According to Martin (1983), this relationship most likely results from strong limiting physiological factors during pregnancy. Martin's equation predicts that, at birth, the brain/body mass ratio in any large-bodied primate should be about 10–11%. We do not know the average body mass of *H. erectus* at birth, but it may have been similar to that observed in *H. sapiens*, as to date the available evidence suggest similar adult body masses for the two species (Ruff et al., 1997). Assuming these conditions, Martin's (1983) allometric equation would predict that the brain size of *H. erectus* at birth would not have been far from that of *H. sapiens*, and most likely, significantly higher than for chimpanzees.[1] This view is supported by the data provided by Leigh, as well as by our own study (Fig. 1). Mojokerto's absolute brain size, at an estimated age of 0.5–1.5 years, is well above the chimpanzee distribution and close to the lower range of the *H. sapiens* distribution. This condition may result primarily from the mother's body size, not from similar developmental curves. Interestingly, if we assume a mean adult brain mass of 789 cc for early *H. erectus* (as computed below), applying a chimpanzee model (40% of adult size at birth—see below) leads to a theoretical EV at birth in the vicinity of 316 cc for early *H. erectus*, which actually is close to the modern human mean at birth.

Proportional endocranial volume

Proportional endocranial volume is also important to consider. It does not obscure the comparisons between species, but gives a different kind of information. Assessment of PEV at different calendar ages tells us 1) about the proportion of cerebral maturation that occurs after birth while an individual is interacting with the environment, 2) at what speed this process develops, and 3) how social and cognitive skills may be affected. It should be emphasized that a model that assumes that *absolute* brain size in *H. erectus* was close to modern human values at an early stage of development does not imply similarities in the subsequent developmental curves, as adult brain size is clearly different between the two species.

When dealing with PEV, there are also some methodological difficulties that potentially obscure the differences between species. These problems are hardly avoidable, but it is important that we remain cognizant of them. The main bias is related to the use of cross-sectional vs. longitudinal data. There is a relationship between body size and brain size, and brain size also shows variation in adults. However, the assessment of

[1] A full-term brain weight for *H. erectus* was estimated from the pelvis of KNM-WT 15000 (Walker and Ruff, 1993) to be 200–240 g. However, there are many uncertainties with this estimate due to the fragmentary nature of the specimen. The pubic regions are almost entirely missing and only small pieces of the sacrum are preserved. The level of sexual dimorphism remains unknown in this species, and the pelvis likely comes from a male. Finally, the specimen is not fully adult.