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Early brain growth in *Homo erectus* and implications for cognitive ability

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Humans differ from other primates in their significantly lengthened growth period. The persistence of a fetal pattern of brain growth after birth is another important feature of human development¹. Here we present the results of an analysis of the 1.8-million-year-old Mojokerto child (Perning 1, Java), the only well preserved skull of a *Homo erectus* infant, by computed tomography. Comparison with a large series of extant humans and chimpanzees indicates that this individual was about 1 yr

(0–1.5 yr) old at death and had an endocranial capacity at 72–84% of an average adult *H. erectus*. This pattern of relative brain growth resembles that of living apes, but differs from that seen in extant humans. It implies that major differences in the development of cognitive capabilities existed between *H. erectus* and anatomically modern humans.

Dental microstructure has been recently used² to determine when in the course of hominid evolution a modern human pattern of dental maturation appeared. Representatives of *H. erectus* have been shown to display a shorter period of dental development, suggesting that a modern human growth pattern evolved more recently. Another important aspect of human growth is 'secondary altriciality'. In most primates, brain growth slows down rapidly after birth¹ whereas hominids have to solve the evolutionary challenge of developing a large brain under substantial physiological, obstetrical and locomotor constraints³. An adaptive solution has been reached by giving birth to offspring with relatively small brains compared with adult brain size. Whereas *Macaca* newborns display an endocranial volume equivalent to 70% of adult size¹, the modern human brain represents only 25% of its adult size at birth and continues to grow at its fast fetal rate during the first year of life. At 1 yr of age the human brain is 50% of its adult size and at 10 yr 95% of the adult brain size is achieved. At birth, apes display an intermediate condition, with an endocranial volume approximately 40% of adult size in the common chimpanzee⁴, with 80% of the adult volume being reached by the end of the first year.

Secondary altriciality has social consequences: modern human children require many years of parental support. It also influences the development of cognitive abilities. Most of human brain growth takes place in an 'enriched environment', while the individual is already interacting with the extra-maternal environment^{5–7}. A prolonged interaction between peripheral somatic areas and developing related sensori-motor cortical areas could be one condition for the development of spoken language. When this important adaptation of the genus *Homo* appeared during the course of

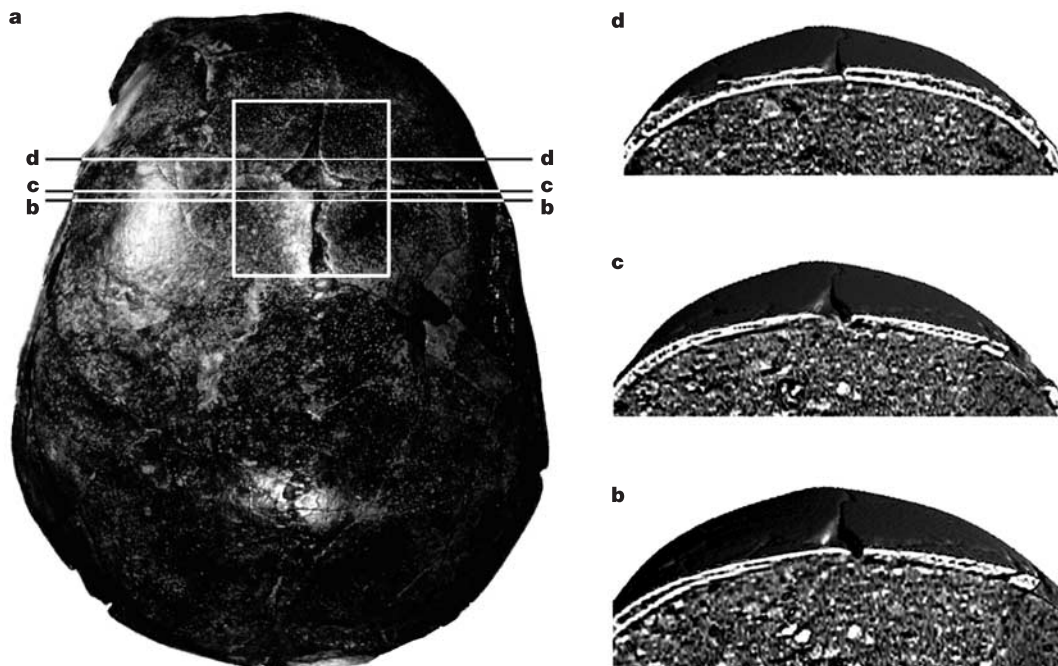


Figure 1 Superior view of the Mojokerto specimen (a) and three-dimensional reconstructions from axial CT scans of the anterior part of the skull (b–d). The location of the coronal cuts are indicated on a. The coronal cuts in b and c, located immediately behind the bregma, display the gap between the two parietals reduced to one compact

table on both sides. The large depression located anteriorly to the bregma on the frontal visible on d results from damage of the outer table. Three-dimensional reconstructions of the skull were made with Voxel-man software (University of Hamburg)²⁸. The photograph in a is from the Senckenberg Museum.

evolution has been much debated^{1–3,8–10}. So far the fossil record has not provided clear evidence of when secondary altriciality developed. In this paper we address this question by analysing the only well preserved brain case of a *H. erectus* infant.

The Mojokerto child was discovered in the Pucangan layers (Perning, Java, Indonesia) in 1936. A hornblende sample extracted from the pumice-bearing layer where the specimen was purportedly found was dated to 1.81 ± 0.04 million years (Myr) ago by the ⁴⁰Ar/³⁹Ar method¹¹. Although this age has been contested, Huffman¹² convincingly argued, on the basis of archival research and primary fieldwork, that the Perning child was found *in situ* in the upper

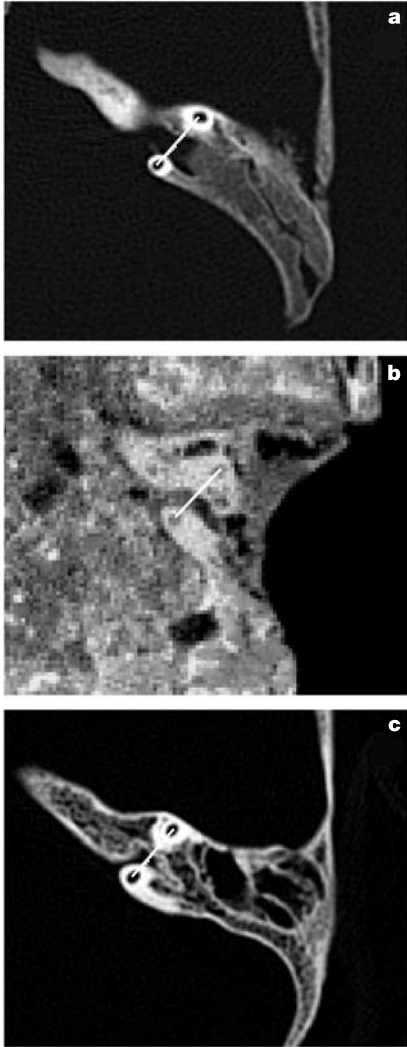


Figure 2 The subarcuate fossa in the right temporal bone of the Mojokerto specimen (**b**) and in two modern specimens (**a**, **c**). The modern specimens are 2 months (**a**) and 18 months (**c**) old. The displayed views correspond to an axial plane parallel to the lateral semicircular canal and are located at the level of maximum development of the fossa. The width of the fossa is measured along a segment joining the two lumens of the anterior semicircular canal (white bar). The exact limits of the fossa in the chosen plane are determined following the method ‘HMH’ defined by ref. 27. The width is expressed as a percentage (SF) of the length of this segment. Left and right sides were averaged for each individual. The modern specimens were scanned with a Siemens Somatom sensation 16 Scanner (Hôpital de Hautepierre, Strasbourg, France). The scans were made contiguously with a field of view of 60×60 mm (512×512 matrix), a slice thickness of 0.6 mm and a pixel size of 0.117 mm. The skull of the Mojokerto child was scanned with a Mx Twin Scanner (Clinique Pasteur, Toulouse, France). The scans were made contiguously in the transverse plane with a field of view of 204×204 mm ($1,024 \times 1,024$ matrix), a slice thickness of 0.5 mm and a pixel size of 0.199 mm.

Pucangan Formation and that the samples used by Swisher *et al.*¹¹ are appropriate as age estimates of this fossil. Consequently, this child may well represent the earliest evidence of hominids in Indonesia, a hypothesis reinforced by the discovery of other hominids of similar age outside of Africa^{13,14}.

The Mojokerto specimen is represented by an almost complete calvaria. Because the specimen lacks dental remains, the determination of its individual age is based on the relative state of development of various cranial structures, and has varied among authors from 18 months to 8 yr old based on modern human standards^{15–18}. The latest estimate of the age of the specimen¹⁹ provided an evaluation of the developmental age using modern human standards, and arrived at an age of between 4 and 6 yr. This evaluation was largely based on the assumption that the anterior fontanelle was closed and on the external aspect of the temporal bone.

By computed tomography (CT) scanning of the Mojokerto calvaria we have been able to re-assess its developmental age. We analysed the maturation of three anatomical areas: the tympanic plate, the bregmatic area of the cranial vault and the subarcuate fossa (a possible criterion of maturation, the sutura mendosa, was not preserved). The development of these three features was scored by known chronological age and by dental stage in a modern human sample comprising 159 immature skulls, between 0 and 8 yr, from the collection of the Strasbourg Medicine Faculty, and on a series of 201 immature *Pan troglodytes* and *Pan paniscus* specimens from the collection of the Royal Museum of Central Africa (Tervuren, Belgium) and from the Museum National d’Histoire Naturelle (Paris, France) (Supplementary Tables S1 and S4).

In contrast with the pattern seen in extant humans and chimpanzees, the Mojokerto tympanic plate is fully ossified, whereas its

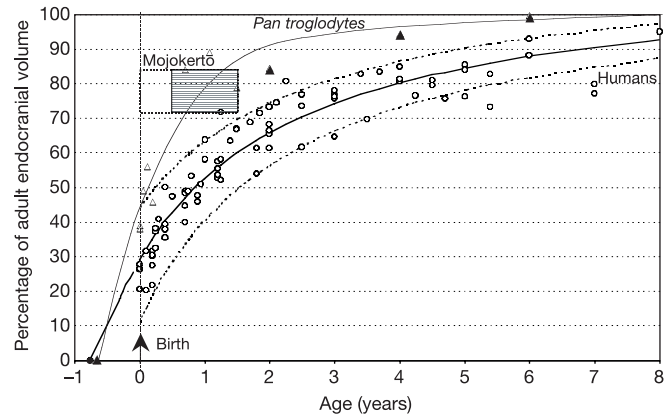


Figure 3 Endocranial volume growth as a percentage of the adult value in Mojokerto, *Pan troglodytes* and extant humans. The Mojokerto specimen is plotted showing the various possibilities in terms of geological and developmental age. The grey area of the Mojokerto box is based only on the estimate from the human model, whereas the white part to the left is based on the estimate from the human and chimpanzee models. The human sample is composed of 93 specimens from the Medicine Faculty of Strasbourg of known calendar age between 0 to 8 yr old. The chimpanzee curve is established from the data from refs 29 and 30 corresponding to a total of 57 specimens between 74 days and 6 yr old (black triangles represent means), and completed by a series of seven individuals of calendar age between birth and 18 months from the Museum National d’Histoire Naturelle (Paris) (white triangles). The endocranial volumes of humans were obtained by direct measurement, and the chimpanzee endocranial volumes either by direct measurements or by medical imaging. The dotted lines correspond to standard errors of estimate around the regression lines (solid lines). The endocranial volume of the Mojokerto specimen was established by medical imaging. On reconstructed sagittal slices separated by 2 mm, the missing portions of the base were reconstructed. The volume was estimated by measuring all the endocranial surfaces with ImageJ software and adding them.

bregmatic area and its subarcuate fossa are still quite immature. The maturation stage of the tympanic plate is not a good age criterion because it can be found open or fully formed in virtually all of the age classes examined (Supplementary Table S5).

The bregmatic area is damaged. Between the anteromedial corners of the parietals a gap of 3.5 mm can either be interpreted as a fontanelle in its final stage of closure or as post-mortem damage. However, even assuming the latter, the parietals are still composed of a single bone table (Fig. 1). In our reference series, an immature pattern of the parietal edges persists only briefly after fontanelle closure, and the development of the diploe near the sagittal suture immediately follows the closure of the anterior fontanelle (Supplementary Fig. S6). In contrast with the modern human condition, the Mojokerto calvaria displays fused hemifrontals with a developed diploe, whereas the parietals are still immature. Similar conditions were met at bregma in our chimpanzee series (Supplementary Fig. S7). The time of closure of the modern human fontanelle was scored by calendar age in our reference series, as well as two other collections: Spitalfields (Natural History Museum, London) and Augier (Musée Orfila, Paris) (Supplementary Tables S2 and S3). In these samples ($n = 297$, between 0 and 5 yr), the closure of the fontanelle occurs between 9 and 34 months.

During infancy and early childhood, the subarcuate fossa is obliterated to form part of the petromastoid canal on the posterior surface of the petrous pyramid. To evaluate the degree of closure of the Mojokerto infant subarcuate fossa, we have measured its width relative to the distance across the anterior semicircular canal (Fig. 2). The bayesian probability of observing in our modern human series a subarcuate fossa similar to that of Mojokerto (SF (see Fig. 2 legend) in the class 20–25%) is $P = 0.20$ between 0–0.5 yr, $P = 0.33$ between 0.5–1 yr and $P = 0.46$ between 1–1.5 yr (Supplementary Table S5). The age determination obtained by analysis of the subarcuate fossa of the Mojokerto specimen is therefore compatible with the lower end of ages estimated from the anterior fontanelle. Taking into account the maturation of the bregmatic area and the subarcuate fossa produces posterior probabilities of calendar ages similar to those obtained with the subarcuate fossa alone (Supplementary Table S5).

If the developmental age of the Mojokerto calvaria is assessed using ape standards, the subarcuate fossa at birth in chimpanzees is generally more closed than it is in the Mojokerto specimen (Supplementary Table S4). The fontanelle is fully closed in all chimpanzee individuals by the age of 3 months and 54% of these individuals also have a fully formed tympanic plate. Combining the results obtained in humans and apes, the most likely age estimate for the Mojokerto specimen is therefore between 0.5 and 1.5 yr, but an age under 0.5 yr cannot be excluded.

A direct measurement of endocranial volume is not possible on the Mojokerto child because the calvaria is filled with matrix. Previous estimates of cranial capacity, using extrapolations from

diameters of the calvaria or direct liquid displacement measurements, ranged from 636 to 730 cubic centimetres^{16,20,21}. CT imaging allowed us to estimate the endocranial volume at 663 cubic centimetres (Fig. 3).

Assuming a geological age for the Mojokerto specimen of approximately 1.8 Myr and a long chronology for the Javan specimens, a comparative sample is provided by early African *Homo erectus s.l.* (KNM-WT 15000 (ref. 22), KNM-ER 3733 (ref. 23) and KNM-ER 3883 (ref. 23)), by the three crania of early *Homo* from Dmanisi (D2280 (ref. 13), D2282 (ref. 13) and D2700 (ref. 14)) and by Sangiran 2 and 4 (Table 1). The endocranial capacity of Mojokerto is about 84% of this adult or sub-adult series. Assuming a short and younger chronological range for the Javan hominids leads to another possible comparison with the series of adult Indonesian *H. erectus* (Sangiran 2, 4, 10, 12, 17, Trinil 2 (ref. 24) and Sangiran IX²⁵) exclusive of the late Ngandong and Sambungmacan specimens. In this case, the cranial capacity of the Mojokerto child is about 72% of the adult size (Fig. 3).

Although our age estimation is primarily based on modern human criteria, the various lines of evidence available on the Mojokerto calvaria more closely match an ape pattern of brain development rate than a modern human one (Fig. 3). On the basis of our modern human sample, the bayesian probability of observing a cranial capacity between 70% and 90% of adult volume is $P = 0.0$ between 0 and 1.0 yr and $P = 0.01$ between 1.0 and 1.5 yr.

Although these results are based on the analysis of only one exceptionally preserved juvenile *H. erectus* skull, they suggest that secondary altriciality was established fairly late in the genus *Homo*, perhaps in the common ancestor of *Homo sapiens* and *Homo neanderthalensis*, which both displayed a very large brain and a reduced pelvic inlet size²⁶. These data also suggest that in *H. erectus* only a short period of brain maturation took place in the extra-maternal environment. This makes it unlikely that early *Homo* had cognitive skills comparable to those of modern humans, and it also implies that complex spoken language emerged relatively late in the course of human evolution. □

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Table 1 Endocranial capacity values for three fossil hominid series

Species	Specimen	Endocranial volume (cc)
Indonesian <i>H. erectus</i>	Sangiran 2	813
	Sangiran 4	908
	Sangiran 10	855
	Sangiran 12	1,059
	Sangiran 17	1,004
	Sangiran IX	850
	Trinil 2	940
African early <i>H. erectus</i> <i>s.l.</i>	KNM-ER 3733	848
	KNM-ER 3883	804
	KNM-WT 15000	880 (adult estimate: 909)
Georgian early <i>Homo</i>	D2280	780
	D2282	650
	D2700	600

cc, cubic centimetres.

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Genetic evidence supports demic diffusion of Han culture

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The spread of culture and language in human populations is explained by two alternative models: the demic diffusion model, which involves mass movement of people; and the cultural diffusion model, which refers to cultural impact between populations and involves limited genetic exchange between them¹. The mechanism of the peopling of Europe has long been debated, a key issue being whether the diffusion of agriculture and language from the Near East was concomitant with a large movement of farmers^{1–3}. Here we show, by systematically analysing Y-chromosome and mitochondrial DNA variation in Han populations, that the pattern of the southward expansion of Han culture is consistent with the demic diffusion model, and that males played a larger role than females in this expansion. The Han people, who all share the same culture and language, exceed 1.16 billion (2000 census), and are by far the largest ethnic group in the world. The

expansion process of Han culture is thus of great interest to researchers in many fields.

According to the historical records, the Hans were descended from the ancient Huaxia tribes of northern China, and the Han culture (that is, the language and its associated cultures) expanded into southern China—the region originally inhabited by the southern natives, including those speaking Daic, Austro-Asiatic and Hmong-Mien languages—in the past two millennia^{4,5}. Studies on classical genetic markers and microsatellites show that the Han people, like East Asians, are divided into two genetically differentiated groups, northern Han and southern Han^{6,8}, separated approximately by the Yangtze river⁹. Differences between these groups in terms of dialect and customs have also been noted¹⁰. Such observations seem to support a mechanism involving primarily cultural diffusion and assimilation (the cultural diffusion model) in Han expansion towards the south. However, the substantial sharing of Y-chromosome and mitochondrial lineages between the two groups^{11,12} and the historical records describing the expansion of Han people⁵ contradict the cultural diffusion model hypothesis of Han expansion. In this study, we aim to examine the alternative hypothesis; that is, that substantial population movements occurred during the expansion of Han culture (the demic diffusion model).

To test this hypothesis, we compared the genetic profiles of southern Hans with their two parental population groups: northern Hans and southern natives, which include the samples of Daic, Hmong-Mien and Austro-Asiatic speaking populations currently residing in China, and in some cases its neighbouring countries. Genetic variation in both the non-recombining region of the Y chromosome (NRY) and mitochondrial DNA (mtDNA)^{13–16} were surveyed in 28 Han populations from most of the provinces in China (see Fig. 1 and Supplementary Table 1 for details).

On the paternal side, southern Hans and northern Hans share similar frequencies of Y-chromosome haplogroups (Supplementary Table 2), which are characterized by two haplogroups carrying the M122-C mutations (O3-M122 and O3e-M134) that are prevalent in almost all Han populations studied (mean and range: 53.8%, 37–71%; 54.2%, 35–74%, for northern and southern Hans, respectively). Haplogroups carrying M119-C (O1* and O1b) and/or M95-T (O2a* and O2a1) (following the nomenclature of the Y Chromosome Consortium) which are prevalent in southern natives, are more frequent in southern Hans (19%, 3–42%) than in northern Hans (5%, 1–10%). In addition, haplogroups O1b-M110, O2a1-M88 and O3d-M7, which are prevalent in southern natives¹⁷, were only observed in some southern Hans (4% on average), but not in northern Hans. Therefore, the contribution of southern natives in southern Hans is limited, if we assume that the frequency distribution of Y lineages in southern natives represents that before the expansion of Han culture that started 2,000 yr ago⁵. The results of analysis of molecular variance (AMOVA) further indicate that northern Hans and southern Hans are not significantly different in their Y haplogroups ($F_{ST} = 0.006$, $P > 0.05$), demonstrating that southern Hans bear a high resemblance to northern Hans in their male lineages.

On the maternal side, however, the mtDNA haplogroup distribution showed substantial differentiation between northern Hans and southern Hans (Supplementary Table 3). The overall frequencies of the northern East Asian-dominating haplogroups (A, C, D, G, M8a, Y and Z) are much higher in northern Hans (55%, 49–64%) than are those in southern Hans (36%, 19–52%). In contrast, the frequency of the haplogroups that are dominant lineages (B, F, R9a, R9b and N9a) in southern natives^{12,14,18} is much higher in southern (55%, 36–72%) than it is in northern Hans (33%, 18–42%). Northern and southern Hans are significantly different in their mtDNA lineages ($F_{ST} = 0.006$, $P < 10^{-5}$). Although the F_{ST} values between northern and southern Hans are similar for mtDNA and the Y chromosome, F_{ST} accounts for 56% of the total among-