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Endocranial Volume and Brain Growth in Immature Neandertals

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Abstract

Microstructural studies have suggested that an extended period of growth was absent in representatives of Homo erectus*, and that Neandertals reached adulthood significantly more rapidly than modern humans. In addition to general rate of growth, a prolonged postnatal period of brain development allows humans to develop complex cognitive and social skills. Conditions in brain growth similar to those observed in extant humans were not established in the first representatives of* Homo erectus*. To assess the degree of secondary altriciality reached by Neandertals, we examined the most complete skulls available for immature Neandertal specimens. The endocranial volumes were evaluated by using equations based on external cranial measurements. The proportional endocranial volumes (PEV) of these fossils were compared to the PEV of known age modern children from Western Europe and to a developmental series of* Pan troglodytes*. We present an estimation of the cranial capacity of Krapina 1. Although Neandertal children are close to the modern variation, the position of the youngest specimens in the upper range of variation led us to propose that Neandertals may have displayed a slightly more primitive pattern with respect to the speed of brain growth.*

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GENERAL RATE OF GROWTH

Humans differ from other primates in their development pattern and particularly in the marked lengthening of their growth processes. These differences have a number of implications, not only in biological terms, but also in terms of social organization, mating strategies, and an extension of the learning period. However, to date, the precise point when a modern growth pattern was established during the course of human evolution still remains obscure. Dental and somatic growth are highly correlated across the primate order *(1–4)*. Thus, advances on the issue of differences in life history between hominin species result primarily from an emphasis placed on dental development and, more specifically, microstructural studies. Recent reassessments of the life history in extinct hominins based on dental studies suggest significant differences in the timing of individual development *(5, 6)*. Based on the analysis of the enamel apposition rate, Dean *et al. (5)* established that an enlarged period of growth was absent in representatives of *Australopithecus* and early *Homo,* and specifically *Homo erectus*. These species more closely align with extant apes than with recent humans.

A long-standing controversy surrounds the question of whether Neandertals shared the prolonged growth periods of modern humans. Dean *et al. (5)* suggested that Neandertals would be at the »fastest« end of modern human variation, and two opposing schemas involving rates of development have recently been proposed for this fossil group. Ramirez Rozzi and Bermúdez de Castro *(6)* established that Neandertals reached adulthood significantly more quickly than modern humans. According to these authors, a short crown formation time in Neandertals indicates that somatic development was not as long as in *Homo sapiens*. The Neandertal anterior teeth grew in about 15% less time than those of Upper Paleolithic-Mesolithic *Homo sapiens*. Neandertals would therefore have taken approximately 15 years to reach adulthood. Similar conclusions had been reached by other authors some years before through observations on a very limited number of specimens *(7)*. In contrast, Guatelli-Steinberg *et al*. *(8)* have challenged these results, suggesting instead that Neandertals did not reach adulthood any more quickly than do modern humans. Specifically, they found that Neandertal imbricational enamel formation times were not faster than those of a living English population.

Ramirez Rozzi and Bermúdez de Castro *(6)* proposed that Neandertals followed a reverse evolutionary trend towards faster dental growth because they differ from other hominins such as *Homo antecessor, Homo heidelbergensis* and even more so in *Homo sapiens* with respect to dental maturation. In their view, this is dependent on brain/body size constraints.

This difference in somatic growth would be consistent with previous work that has suggested that characteristic differences in cranial and mandibular shape between Neandertals and modern humans arose very early in development *(9)*. On the contrary, Guatelli-Steinberg *et al. (8)* concluded that, if anterior tooth crown formation periods reflect overall growth periods, then by extension, Neandertal somatic growth appears to be encompassed within the modern human range of interpopulation variation.

SECONDARY ALTRICIALITY

In addition to general rate of growth, another important aspect of human growth is referred to as »secondary altriciality« *(10, 11)*. Humans differ from other primates not only in their extended growth period, but also in the relative speed of development of their brain when compared to speed of development in the rest of the body. Because the brain represents a very »expensive tissue« in terms of physiological costs *(12),* its size at birth is likely constrained by the basal metabolism of the mother *(11)*. In addition, the pelvis size and morphology are also strongly constrained in bipedal hominins *(13)*. As a result the size of the brain at birth has been under a strong selection pressure in recent human evolution and the increase of adult brain size in recent hominins was made possible only by extending the rapid fetal increase of the absolute size of the brain for a relatively long time after birth.

This phenomenon is invoked to explain some unique aspects of brain growth in human children compared to other primates. In most primates, brain size reaches a high proportion of the final adult size before birth (70% in macaques, for example) and brain growth slows rapidly after birth *(11)*. An intermediate situation is found in the common chimpanzee, where 45% of the adult size is reached at birth, and 80% of the adult volume is reached by the end of the first year. In humans at birth, brain size is on average only 25% of the adult size and a high fetal growth rate is sustained a full year after birth. At one year of age, the brain is still around only 50% of its adult size, and it is not before 8 years that it reaches 90% *(14)*. A re-sampling method and a large data set *(15)* provide further evidence for our conclusions that humans and chimpanzees do not achieve the same proportion of brain growth *in utero*. Using brain weights, the results obtained by Desilva and Lesnik *(15)* differ from what we obtained on endocranial capacity by only a few percent. This has been confirmed again by the compilation of many measurements by Alemseged *et al*. *(16)*.

Post-natal volume increase in humans is an outcome primarily of the development of white matter resulting from the development and maturation of cerebral connections. Most of this development takes place in the complex extra-maternal environment while the individual is already interacting with its surroundings, and the way that the human brain grows has important consequences in the development of cognitive and social skills. During normal ontogeny, there is an extended period of development, during which synapses are retained or eliminated in response to sensory stimulation or motor activity. Abnormally accelerated brain growth in humans results in a severe impairment of cognitive skills, and a dramatic growth spurt in the first year of life leads to social and cognitive impairments, as suggested by Courchesne *et al*. *(17)* in their studies of children affected by severe autism.

Determining the time of emergence of a modern pattern of secondary altriciality in the course of human evolution is therefore of great interest and this question has been extensively debated. One main problem in assessing this issue results from the fact that we can rely only on cross-sectional studies, and that adult brain size displays large degrees of variation, which may be even more marked in species displaying high levels of sexual dimorphism. In addition to the uncertainty resulting from the evaluation of the calendar age at death of immature individuals, their proportional brain size can be computed only relative to a mean of the known adults. This results in an artificial increase in the observed variability and overlap between taxa. Computations based on the immature *Australopithecus africanus* from Taung, South Africa suggest that it conforms to an ape model. Recent evidence from the description of the Dikika juvenile *Australopithecus afarensis (16),* however, suggests large possible variability, if not an intermediate situation be-

TABLE 1

Endocranial Volume (EV) and Proportional Endocranial Volume (PEV) in fossil specimens according to dental age.

	Dental Age (y)	Computerized-assisted measurement of EV (cc)	Mathematical measurement of EV (cc)	PEV (%)
Dederiyeh 2	2		1105	74
Pech de l'Azé 1	2.5		1199–1213 (m=1206)	80–81
Roc de Marsal	3	1325		88
Subalyuk 2	3		1166	78
Devil's Tower	4 – 5	1400		93
Engis 2	4 – 5	1440		96
La Quina 18	6 – 8		1257–1275 (m=1266)	84–85
Krapina 1	6 – 8		1236–1350 (m=1293)	83–90
Teshik–Tash	8 – 10		1495–1522 (m=1507)	100–102
Skhul 1	4 – 4.5		1130–1154 (m= 1141)	73–75
Qafzeh 10	6		1265–1271 (m=1268)	82

The means of the range of variation for the EV are expressed in parentheses

tween extant humans and apes. When compared to only female adult specimens (AL162-28, Al 228-1), the proportional endocranial volume (PEV) of Dikika 1 varies between 69 and 85%, in the region of overlap between *Pan troglodytes* and humans. Using computed tomography, we were recently able to investigate the calendar age and endocranial capacity of the only known juvenile *Homo erectus* skull: the Mojokerto (Perning 1, Indonesia) specimen *(18)*. A re-investigation at the site and radiometric dating point to a very Early Pleistocene age for the specimen, which may approach 1.8 million years *(19–21)*. In addition to features visible externally such as the maturation of the tympanic plate, CT scanning has allowed us to examine internal cranial features indicative of the stage of maturation for this individual. In particular, we focused our study on the bregmatic area and the *fossa subarcuata*. Our study indicates that, even by modern human standards, this individual was most likely less than 1.5 years old at death. This age determination implies a high proportional brain size in Mojokerto, closer to that observed in living apes than in average extant humans of the same calendar age *(18)*. From our study, we concluded that conditions in brain growth similar to those observed in normal extant humans were established relatively late in the course of hominin evolution *(14)*.

THE CASE OF NEANDERTAL SPECIMENS

In order to assess the degree of secondary altriciality reached by Neandertals, we selected the most complete skulls of immature Neandertal specimens to illustrate the pattern of brain growth during the first years of life. We also selected 2 young specimens from the early anatomically modern human groups of Qafzeh/Skhul. Individual ages were estimated for each specimen based on modern standards in terms of degree of dental calcification and eruption *(22–28)*. This approach is the most conservative with regard to the debates on the speed of dental development in Neandertals.

For the Neandertal sample, the youngest specimens are Dederiyeh 2, estimated to be around 2 years *(29)*, Pech-de-l'Azé 1 around 2.5 years *(30)*, Roc de Marsal and Subalyuk 2 with a dental age of 3 years *(31, 32)*. Disagreements have surrounded the age of Devil's Tower, in which traditional methods of assessing dental developmental status have been compared to techniques based upon histological observations *(7, 33–37)*. A range of age variation between 4 and 5 years old is proposed here for this specimen. The same range of dental age has been established for Engis 2 *(34, 38)*. Age assessment of Krapina 1 is problematic due to the lack of any associated teeth. A range variation between 6 and 8 years was proposed using a series of developing cranial features *(39)*. The same age variation is used for the dental age of La Quina 18 *(25, 40)*. The oldest Neandertal specimen in terms of calendar age is Teshik-Tash, around 8-10 years *(41)*.

The dental age of the two anatomically modern specimens, Skhul 1 and Qafzeh 10 are estimated to be 4–4.5 years, respectively *(42)* and around 6 years *(43)* (Table 1). In Figure 1, the horizontal arrows represent the range of age variation for the fossils and the median value is indicated by a point.

Individual ages of our Neandertal sample range from 2 to 10 years old, but it should be noted that it is during the first post-natal years that differences among primates can be observed in terms of proportional brain growth. In other words, the youngest individuals are the most likely to show differences from extant humans, as after five years, humans and non-humans tend to increasingly overlap (Figure 1). If Neandertals grew around 15%

TABLE 2

Endocranial volume estimations for fossil immature specimens with Coqueugniot (1994) equations.

	Equations for 0–15 years old children		Equations for 4–15 years old children	
	M1, M8 M17*	M1, M8, M20*	M1, M8 M17*	M1, M8, M20*
Dederiyeh 2		1105 cc		
Pech de l'Azé 1	1199 cc	1213 cc		
Subalyuk 2		1166 cc		
La Quina 18	1274 cc	1260 cc	1275 cc	1257 cc
Teshik-Tash	1495 cc	1495 cc	1516 cc	1522 cc
Skhul 1	1138 cc	1154 cc	1130 cc	1144 cc
Qafzeh 10	1271 cc		1265 cc	

* after measurements from Ishida and Kondo *(29),*(Dederiyeh 2); Ferembach *(30)* (Pech de l'Azé 1); Pap *et al. (59)*; Martin *(40)* (La Quina 18); Gremjackij *(41)* (Teshik-Tash); McCown and Keith *(42)* (Skhul 1) and Tillier *(43)* (Qafzeh 10).

faster than moderns as proposed by Ramirez-Rozzi and Bermúdez de Castro *(6),* then our ages should be reduced accordingly.

Considering the fragmentary nature of many specimens, we evaluated the endocranial volumes by using different equations that deduce this volume from external cranial measurements, rather than direct volume measurements or estimates. In the literature, few equations specifically take into account the distinctive shape and morphology of immature skulls *(44–48)*. Some of these equations have proven to be reliable and have been validated by previous studies *(49)*. For each individual, proportional endocranial volume (PEV) was computed by dividing the estimated individual endocranial volume by the average adult endocranial volume, not taking into account the sex of the individuals, as it is impossible to establish this on immature specimens. The PEVs were calculated with an adult value of 1498 cc (n=14) for Neandertals *(50)* and a value of 1545 cc calculated from 5 specimens: Skhul 4, Skhul 5, Skuhl 9, Qafzeh 6 and Qafzeh 9 *(51)*. These data are compared in Figure 1, with the PEV of populations of recent modern humans from western Europe established on a developmental series of 85 specimens with known calendar age from the Department of Anatomy of the School of Medicine Strasbourg, France, and with a developmental series of *Pan troglodytes*. The age distribution of the children is 0 to 7.8 years old. The chimpanzee curve was established from the data from Zuckerman *(52)* and Schultz *(53),* corres-

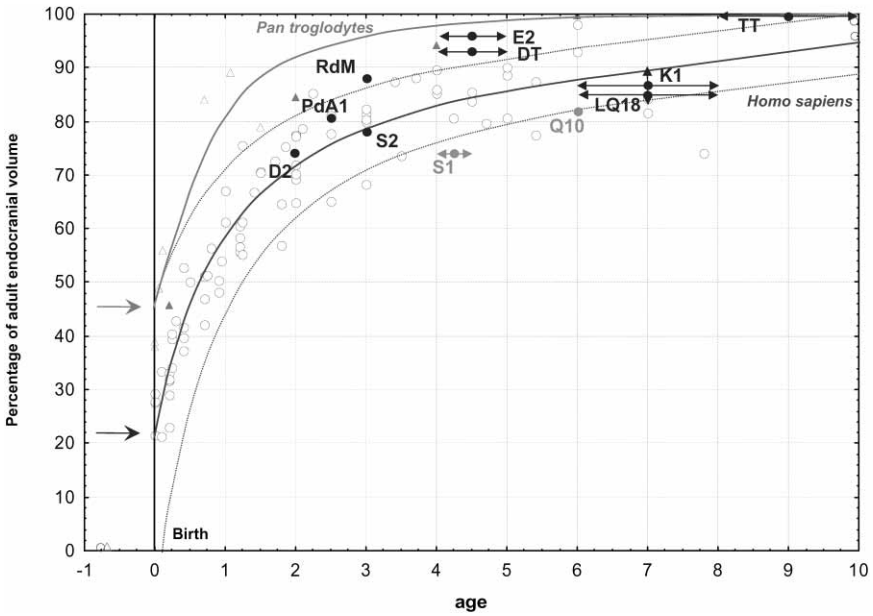

Figure 1. *Endocranial volume growth in percentage of the adult value in Qafzeh-Skhul and Neandertal immatures according to proportional endocranial volume curves of* Pan troglodytes *and extant humans (D2: Dederiyeh 2; PdA1: Pech-de-l'Azé 1; RdM: Roc de Marsal; S2: Subalyuk 2; DT: Devil's Tower; E2: Engis 2; K1: Krapina 1; LQ18: La Quina 18; TT: Teshil-Tash; S1: Skhul 1; Q10: Qafzeh 10).*

TABLE 3

Endocranial volume estimations for Krapina 1 with equations specific to children.

Poissonnet *et al*. (1978) equations specific to children	CC= 91,71*(M9/10) + 113,72*(M29/10)–1124*	CC= 10,799*(M9/10*M29/10) + 290*	CC= 16,185*(M27/10*M30,3/10)–112*	Mean
Endocranial volume (cc)	907.6	1348.3	1452.5	1236.1

* after measurements from Minugh-Purvis *et al.* (39)

TABLE 4

Endocranial volume estimations for Krapina 1 with equations specific to adults and Neandertal specimens.

Poissonnet *et al*. (1978) equations specific to adults	CC = 147,25*(M29/10) + 135,75*(M9/10) –1489*	CC = 13,92*(M29/10)*(M9/10)–43–100*	CC = 11,863*(M27/10)*(M30,3/10)+271+100*	Mean
Endocranial volume (cc)	1311.6	1221.2	1517.7	1350.1

* after measurements from Minugh-Purvis *et al.* (39)

ponding to a total of 57 specimens between 74 days and 6 years old (full triangles represent means), completed by a series of 7 individuals of calendar age between birth and 18 months from the Museum National d'Histoire Naturelle (Paris) (empty triangles) *(18)*. The endocranial volumes of humans were obtained by direct measurements, the chimps' endocranial volume either by direct measurements or by imaging techniques. On Figure 1, the dotted lines correspond to standard errors of estimate around the regression lines (solid lines).

The endocranial volumes obtained after computerized reconstruction of fossil skulls are the nearest values of the exact cranial capacity: the missing parts of the endocranial cavities are completed by symmetry or »morphing« of the existing parts. With this procedure, good endocranial volume estimates were determined for Roc de Marsal, Devils' Tower and Engis 2 *(54)*.

Because few fossil immature specimen were computer-assisted reconstructed, the endocranial volumes of most of our fossil sample were calculated from equations established by one of us (HC) *(48),* when the preservation of the fossil skulls was sufficient. These formulas were established on an immature sample of 48 specimens. With these equations, different cranial capacities can be calculated in function of dental age (before 4 years and after 4 years at death) and as a function of cranial length, width and height (M1, M8, M20 and M17, after measurements of Martin and Saller *(55)*. We used these equations to estimate the endocranial volume of Dederiyeh 2, Pech de l'Azé 1, Subalyuk 2, La Quina 18, Teshik-Tash and the two early anatomically modern specimens Skhul 1 and Qafzeh 10. The entire range of endocranial volume variation is represented on Figure 1.

The state of preservation of the juvenile Krapina 1 skull does not permit a direct measurement of endocranial volume or an indirect estimation with the use of previously published equations. We used the formulas proposed by Poissonnet *et al. (47)* established for isolated bones to calculate an estimation of the endocranial volume of the Croatian fossil. We selected equations based on the frontal and parietal bones and used measurements of Krapina 1 from Minugh-Purvis *et al. (39):* minimum frontal breadth (M9), nasion-bregma chord (M29), bregma-lambda chord (M27), and lambda-asterion chord (M30.3).

Poissonnet *et al*. *(47)* proposed specific equations for immature skulls, established with a sample of 34 specimens between 2 and 16 years old. With the measurements available on the fossil, only 3 of the equations were appropriate for use here. The mean estimated endocranial volume for Krapina 1 is then 1236 cc (Table 2).

Poissonnet *et al*. *(47)* also proposed equations for estimating adult cranial capacity with a specific coefficient of correction for fossil hominids, and among others, for Neandertal specimens. Because the age at death of Krapina 1 was 6–8 years old *(39, 56),* it is reasonable to accept that the endocranial volume of the fossil is not very distant from its adult value, and we therefore used the equations established for adults as the upper limit for the estimation of the endocranial volume of Krapina 1 (Table 3).

We propose an estimation for the endocranial volume of Krapina 1 between 1236 and 1350 cc. This is a rather large range of variation; the preservation of the specimen, however, does not allow a more precise estimation at present. Moreover, these estimations fit with the cranial capacity published for immature Neandertal specimens around the age of Krapina: specifically the endocranial volume of La Quina 18 (see above) and the volume of Teshik-Tash (see above).

CONCLUSION

It could be tempting to explain the marked differences in endocranial volume observed in immature Neandertals by the expression of a distinct sexual dimorphism in young Neandertal specimens *(7, 35)*. However, extant humans also display strong variation in endocranial volume (Figure 1), and this hypothesis was falsified by results of comparisons of metric features between Neandertals, early anatomically modern and Upper Palaeolithic immature specimens *(43)*.

Our assessment based on the available fossil evidence (Figure 1) leads to the conclusion that Neandertal children widely overlap with the range of modern variation. This does not come as a surprise, as Neandertals display an adult cranial capacity and inlet diameter of the pelvis not much different from those observed in *Homo sapiens (50, 57)*. It is quite intuitive that Neandertals and modern humans, as well as their common ancestors, exhibited a fairly well established modern pattern of secondary altriciality. This adaptation likely allowed the spectacular enlargement of adult endocranial volume observed in Pleistocene hominins after 500,000 BP, independently of any marked increase in body size *(12; see also comments in 14)*. However, although this observation is based on a small number of specimens, it is to be noted that the youngest Neandertals of our series are systematically placed above the average values observed in our modern series. For Roc de Marsal, Devil's Tower, and Engis 2, the PEV is even partly located beyond the upper limit of our modern range. The endocranial capacity values of La Quina H18 and Krapina 1 are situated within the lower part of the modern variation. However, as discussed above, we consider these older individuals as less significant. Teshik-Tash displays a high value for its PEV but the cranial capacity at around 9 years old is already practically the same as the adult value.

In conclusion, even if some have concluded that Neandertals demonstrated a pattern of secondary altriciality identical to that of modern humans *(4, 58),* it might be suggested that, although Neandertals were indeed close to the conditions observed in a modern sample, they may have displayed a slightly more primitive pattern with respect to the speed of brain growth. Further, the view supported by some studies *(5, 6, 7)* that Neandertals displayed faster development for general somatic growth would emphasize this difference between Neandertals and modern humans by displacing the Neandertal distribution of PEV toward younger calendar ages. In an opposite direction, and although based only on two individuals, the values of PEV for the early modern humans from Qafzeh 10 and Skhul 1 lie under the average values observed in our modern comparative sample.

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