TECHNICAL COMMENT

PALEOANTHROPOLOGY

Comment on "The growth pattern of Neandertals, reconstructed from a juvenile skeleton from El Sidrón (Spain)"

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Rosas *et al*. (Reports, 22 September 2017, p. 1282) calculate El Sidrón J1 to have reached only 87.5% of its adult brain size. This finding is based on an overestimation of Neandertal brain size. Pairwise comparisons with a larger sample of Neandertal fossils reveal that it is unlikely that the brain of El Sidrón would have grown appreciably larger.

Rosas *et al*. (*1*) are to be congratulated for their discovery and whole-body analysis of El Sidrón J1—an important addition to our understanding of Neandertal paleobiology, growth, and development. Although Rosas *et al*. present a rich, whole-body treatment of El Sidrón J1, an emphasis was made in the paper—and widely reported by the science media (*2*)—that at 7.7 years of age, this individual had only achieved 87.5% of its total brain volume and was therefore still growing its brain. This finding would be quite extraordinary, given that 95% of brain growth is achieved in modern human children by the age of 6 to 7 years (*3*, *4*).

The cranial capacity estimated for El Sidrón J1 is 1330 cc (*1*). Careful and clever analysis of bone surface remodeling on the J1 occipital demonstrates that this region of the skull was still osteogenic, consistent with the juvenile status of the individual. The relationship between occipital remodeling and the magnitude of remaining brain growth is unknown, however. Future work examining whether evidence for occipital remodeling is present in juvenile modern humans or Neandertals who are >8 years old (e.g., Teshik-Tash, Le Moustier 1) and have reached adult brain volume will be informative. The authors propose that only 87.5% of full brain capacity had been reached in El Sidrón J1 on the basis of a Neandertal adult brain volume of 1520 cc (*1*). This adult value is an overestimate.

The use of 1520 cc for adult Neandertal brain size is explained as an average of five different studies [table S32 of (*1*)]. The largest adult cranial capacity average used to create this consensus value (*5*) is an average of only six adult Neandertal crania (Amud, Shanidar 5, La Ferrassie, La Chapelle, Spy 2, Tabun C1), which also happen to possess some of the largest brain sizes of the known Neandertals (Table 1). The lowest of the average Neandertal cranial capacities (1494 cc) used to create the consensus average derives from a source that restricts its analysis to nine Würm Neandertals (*6*). However, there is a math error in that paper, and the average of the listed cranial capacities should have been 1468.7 cc, not 1494 cc. Additionally, using values from Holloway *et al*. (*7*) for those Neandertals would result in an average cranial capacity of 1438.3 cc. A third value of 1498 cc, based on Holloway *et al*., is used to generate the consensus average (*1*). In Holloway *et al*., an average for *Homo sapiens neanderthalensis* is reported as 1487.5 ml in appendix I and 1427.2 ml in appendix II. The 1427.2-ml value is almost identical (1428 ml) to the average of reported adult values in the text of Holloway *et al*. However, Holloway *et al*. also attribute fossils typically assigned to *Homo sapiens* [Jebel Ihroud (n = 2) and Skhul (n = 4)] to Neandertals. When these are removed, the average Neandertal adult cranial capacity in Holloway *et al*. is 1414.8 ml. Given these problems with the values used to generate the consensus average of cranial capacity in adult Neandertals, it is necessary to recalculate the likely percentage of adult brain size achieved by the El Sidrón juvenile.

When all adult crania assigned to Neandertals (n = 26) are used (Table 1), the average adult brain size is 1388 cc, and the El Sidrón juvenile had reached 97.4 ± 12.6% of its full growth. When those crania listed specifically in table S32 of (*1*) are used, the average adult Neandertal brain is 1438 cc and the El Sidrón juvenile had reached 94 ± 12.6% of its adult cranial capacity. To account for temporal changes in Neandertal cranial capacity (Fig. 1), it is reasonable to only use crania from the later (<115,000 years ago) Würm Neandertals, which average 1459 cc. Using this value, the El Sidrón juvenile had achieved 92.5 ± 12.0% of its full growth. However, because the dimensions of Krapina 1 are used to help reconstruct the El Sidrón J1 cranium (*1*), it would make sense to include the Krapina fossils as well, in which case the average Neandertal adult brain was 1437 cc and El Sidrón J1 had reached 93.9 ± 11.8% of its brain growth.

Note that in every case, El Sidrón J1 is within the 95% confidence interval of the mean for 100%

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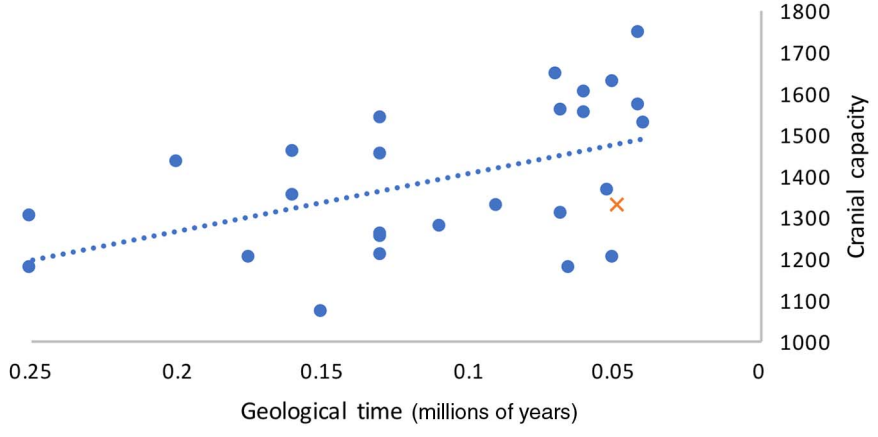

Fig. 1. Neandertal brain size evolution. Adult cranial capacity is known for 26 Neandertals (blue circles). Notice that there is a slight but statistically significant (r = 0.49, P = 0.006) increase in brain size over the course of Neandertal evolution. El Sidrón J1 (red ×) falls comfortably within the range of adult cranial capacities in late Würm Neandertals.

Table 1. Neandertal cranial capacities. Würm Neandertals (living <115,000 years ago) are in italics. Cranial capacities are from (*1*, *7*, *11*–*13*).

Specimen	Cranial capacity	Developmental age	Percent of El Sidrón juvenile cranial capacity
Saccopastore 1	1174	Adult	113.3
Saccopastore 2	1300	Adult	102.3
Reilingen	1430	Adult	93.0
Biache	1200	Adult	110.8
Apidima 2	1454	Adult	91.5
Fontechevade II	1350	Adult	98.5
La Chaise	1065	Adult	124.9
Lazaret	1250	Subadult	106.4
Krapina 1	1293	6 to 8 years	—
Krapina 2	1450	Subadult	91.7
Krapina 3	1255	Adult	106.0
Krapina 5	1535	Adult	86.6
Krapina 6	1205	Adult	110.4
Tabun C1	1271	Adult	104.6
Subalyuk	1187	3.2 years	—
Ganovce	1320	Adult	100.8
Teshik-Tash	1525	~9 years	—
Roc de Marsal	1325	3 years	—
La Ferrassie	1640	Adult	81.1
Spy I	1305	Adult	101.9
Spy II	1553	Adult	85.6
La Quina 5	1172	Adult	113.5
La Quina 18	1200	6 to 8 years	—
Mezmaiskaya	429	Infant	—
Engis 2	1362	3.2 years	—
Shanidar 1	1600	Adult	83.1
Shanidar 5	1550	Adult	85.8
Monte Circeo	1360	Adult	97.8
Gibraltar–Devil's Tower	1400	4.6 years	—
Gibraltar–Forbes Quarry	1200	Adult	110.8
La Chapelle	1625	Adult	81.9
El Sidrón J1	1330	7.7 years	—
Dederiyeh 1	1096	1.55 years	—
Dederiyeh 2	1089	2.0 years	—
Pech de l'Aze	1135	2.5 years	—
Amud	1740	Adult	76.4
Le Moustier 1	1565	Subadult	85.0
Le Moustier 2	418	Infant	—
Feldhofer	1525	Adult	87.2

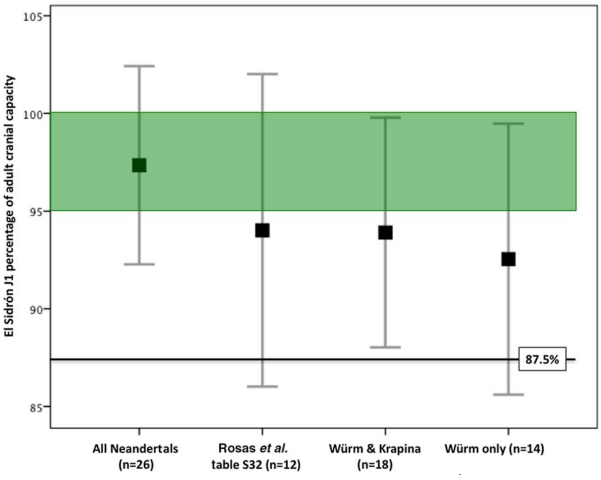

Fig. 2. El Sidrón J1 relative brain size. The cranial capacity of El Sidrón (1330 cc) was divided by all adult Neandertal cranial capacities to calculate a percentage of adult brain size achieved by the age of the individual's death (7.7 years). The mean value (black square) is plotted along with the 95% confidence interval of the mean (gray bars). Note that the percentage of brain size achieved at death in a similarly aged modern human (95 to 100%; green highlighted range) either encompasses the mean (for all Neandertals) or very nearly does. These data suggest that El Sidrón J1 had achieved significantly more of its adult cranial capacity than the 87.5% reported by Rosas *et al*. (*1*), and likely had little remaining brain growth.

brain growth (Fig. 2). The only statistically supported way in which the El Sidrón juvenile could be used as evidence for continued brain growth in a 7.7-year-old Neandertal is if his cranial capacity (1330 cc) is compared exclusively with the largest half of the Würm Neandertals. Accurately identifying the sex of Neandertal crania is fraught with challenges, and using just the largest-brained Neandertals as a comparative male sample biases the results and borders on circular reasoning. Given both spatial and temporal variation in Neandertal brain size, I would recommend caution in inferring Neandertal brain ontogeny from El Sidrón J1 until the average adult brain size in this specific population of Neandertals at El Sidrón is better understood.

There is inherent error in using isolated specimens and cross-sectional data to infer longitudinal patterns. Therefore, attempts to reconstruct the pattern of Neandertal brain growth should incorporate all of the available data. Consider, for instance, that the ~3-year-olds (*8*) Roc de Marsal (1325 cc) and Engis 2 (1362 cc) have brain sizes similar to, or slightly larger than, El Sidrón J1. The 4.6-year-old Devil's Tower child (*8*) has a cranial capacity of 1400 cc, exceeding that found in the developmentally older El Sidrón J1. These specimens should not be used to argue for early cessation of Neandertal brain growth any more than El Sidrón J1 can be used for extended brain growth. Instead, when all of the currently available data are plotted (Fig. 3), Neandertals and modern humans present very similar brain growth curves. Neandertals therefore probably did experience human-like extended brain ontogeny [(*9*), but see (*10*)]. On the basis of the evidence currently available, it is quite likely that El Sidrón J1 had very nearly reached his full brain volume.

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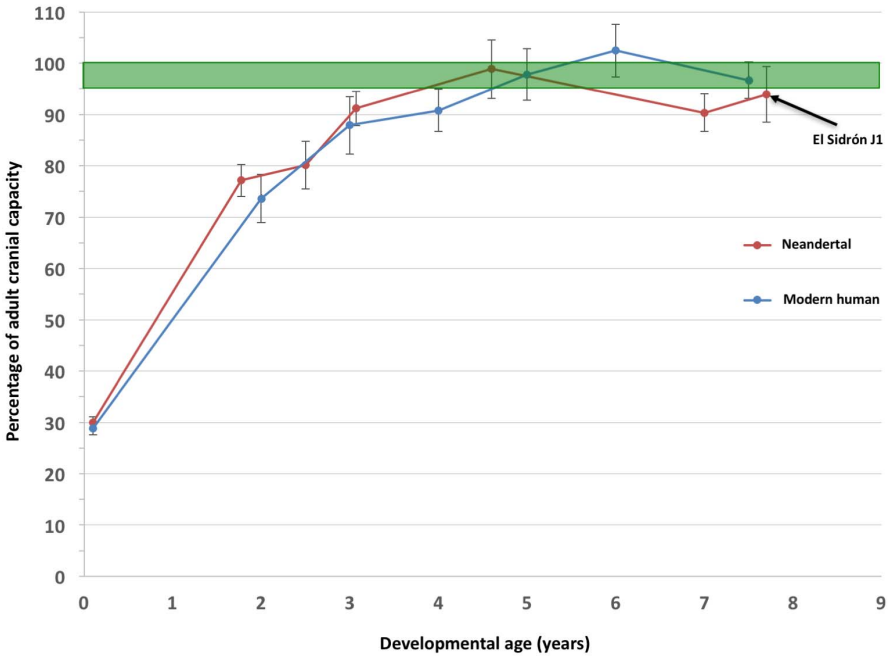

Fig. 3. Neandertal brain ontogeny. El Sidrón J1 is one of 13 known juvenile Neandertal crania (Table 1). Developmental ages of these individuals were based on data in (*1*, *8*, *13*, *14*). These juvenile cranial capacities were each divided by the 18 Würm + Krapina adult cranial capacities to calculate a Neandertal brain growth curve. Error bars indicate 95% confidence interval of the mean of the percentage of brain growth achieved by that chronological age in Neandertals and modern humans. Human data were drawn from (*15*). Notice the similarities between human and Neandertal brain development [see also (*9*)]. Although El Sidrón J1 is slightly smaller than expected, in this broader context it appears best interpreted as normal variation in Neandertals. Accepting the premise that El Sidrón J1 (at age 7.7 years) is evidence for extended brain growth in the Neandertals would also necessitate accepting that Neandertals essentially ceased brain growth between the ages of 3 and 7.7 years, only to resume again.

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