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Commentary: Human brains *have* shrunk: the questions are *when* and *why*

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A Commentary on:
Human brains *have* shrunk: the questions are *when* and *why*

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1 Introduction

Brain size is a very important topic for paleoneurology and paleoanthropology, even if this topic has generated more controversies than answers, and there is little consensus on the actual dynamics of brain size evolution. A recent example of these controversial issues is the human brain reduction from the Late Pleistocene/Holocene to the modern days, supported by the analysis of a large compilation of fossil and recent human crania in DeSilva et al. (2021, 2023), but not confirmed by the analysis on a subset of the same data performed by Villmoare and Grabowski (2022), which have found that there is no reduction in brain size in modern humans since the origins of our species. Indeed, DeSilva et al. (2021) determined changepoints in the time evolution of human cranial capacity using the package changepoint (Killick and Eckley, 2014) and segmented regression models (Muggeo, 2008). They found three changepoints, two positive rate changes in hominin brain evolution and one very recent negative rate change. The first, 2.1 million years ago, coincided with the early evolution of the genus *Homo*. The second, 1.5 million years ago, related to technological innovations seen in the archaeological records. The last changepoint, a negative rate change, is regarding the recent *Homo sapiens* evolution at an age of 3±1 ka. Villmoare and Grabowski (2022) argued that the dataset of DeSilva et al. (2021) was inadequate, and the mean endocranial volume of *H. sapiens* for age ~0.1 ka was not correct. Due to the scarcity of fossils that, for *H. sapiens*, spans a huge interval (300 ka), Villmoare and Grabowski (2022) argued that a dataset with too many data in the range age ~0.1 ka (N=578) over a total of N=836 is time unbalanced towards recent ages, biasing the research of changepoints, leading to a false negative rate change in *H. sapiens*' endocranial-volume evolution for the 3–5 ka age. DeSilva et al. (2023) replied to the criticisms of Villmoare and Grabowski (2022) changing partially the endocranial volume dataset and confirming the reduction in the last 3–5 ka age. This surprising recent brain reduction was linked by the authors to the ability to store information externally in social groups, which relaxed the strong forces of selection for maintaining large brains. In particular, according to DeSilva et al. (2021), also studies of ants' social systems could aid in interpreting patterns of brain evolution identified in humans.

These controversial conclusions should be related to the fact that *H. sapiens*' cranial capacity can differ by over 1,000 cc (Holloway et al., 2004). Indeed, these big differences of endocranial volume within our species complicate the study of cranial capacity's evolution, starting from few available fossil samples. To handle data consistent with the analysis reported in DeSilva et al. (2023), we summarize the statistical results of some key studies about the endocranial volume of contemporary *H. sapiens* (age ~1 ka). Beals et al. (1984) analyzed data on 5,288 crania from 122 different ethnic groups and reported an endocranial volume of 1,349 ± 78cc. Henneberg (1988) indicated 1,387cc for a sample N=245. The Dekaban and Sadowsky (1978) adult dataset (N=3,399) indicates an average value of 1,334.5 ± 205.9cc. A fundamental point to be considered is that the distribution of endocranial volumes of adult humans has a bimodal shape, with two most frequent values, one for male and the other for female. Rushton (1994) reported in Table 1 of his paper average cranial capacities for individuals of almost all geographical regions of the earth. He found a value of 1,401 ± 42cc for men and 1,186 ± 53cc for women. The difference of the two means is greater than two standard deviations, implying a distribution of endocranial volumes characterized by two separate maxima. By considering studies with an equal sex representation, average endocranial volumes vary between 1,335 ± 206cc (Dekaban and Sadowsky, 1978; N=3,399) and 1,344 ± 137cc (Ho et al., 1980; N=1,261). The average of these two datasets is 1,337 ± 187cc, very close to the value indicated by Beals et al. (1984). Thus, we can consider also this last dataset balanced in terms of sex representation, obtaining a final average, for N=3,399 + 1,261 + 5,288 = 9,948 adult individuals, equal to 1,343 ± 129cc. DeSilva et al. (2023) reported, for the more recent age of 0.1 ka, N=415 entries with an average value of 1,297 ± 152cc. Adding this last dataset to the above ones, a final dataset of N=10,363 is obtained, with an average endocranial volume of 1,341 ± 130cc, statistically well representative of the endocranial volume of contemporary humans (age ~0.1 ka). Supplementary Figure S1 shows the data reported in DeSilva et al. (2023) excepted the values corresponding to 0.1 ka, substituted with the N=10,363 average value. Supplementary Figure S1 clearly shows that the endocranial volumes of *H. sapiens*, corresponding to other ages than 0.1 ka, fall mainly over the 0.1 ka value. A fossil of the past could have an endocranial volume value that differs from the 0.1 ka average value both due to the natural variability of the cranial capacity of humans and due to a time evolution of the cranial capacity. Supplementary Figure S2 shows the differences, with respect to the mean value obtained at age ~0.1 ka (N=10,363), of all the fossils corresponding to the *H. sapiens*. Numerical values have been reported in Supplementary Table S1. The unequal sex representation of endocranial volumes for the few fossils available, belonging to a specific age, could become a source of bias when studying time evolution of the *H. sapiens*' cranial capacity.

2 The condition of equal sex representation of endocranial volumes

Distribution of endocranial volumes of adult humans has a bimodal shape, with two most frequent modes or values, one for male and the other for female (Rushton, 1994). An equal sex representation of cranial capacity of a dataset should lead to a histogram distribution characterized by two maxima (male and female modes) of nearly the same height. Supplementary Figure S3 shows a histogram of the N=26 cranial capacity data for *Homo neanderthalensis* reported by (DeSilva et al., 2023), divided in pre- and post-Würm ages. The histograms for both periods confirm that the endocranial volume distribution also for *H. neanderthalensis* is bimodal, as for *H. sapiens*. The subset of data of *H. neanderthalensis*, reported by DeSilva et al. (2023), is quite well-balanced in terms of sex representation. Conversely, analyzing the *H. sapiens*' data, we should note that one of the subsets consisting of N=25 specimens found at Afalou, Algeria (Vallois and Hallam, 1952), dated at an age of 11.5 ka, just at the beginning of the Holocene, is not well-balanced in terms of sex representation. Supplementary Figure S4 shows the histogram of these N=25 endocranial volumes. It can be noted that this subset of data is strongly unbalanced in terms of sex representation, most probably 5 females and 20 males, as it can be estimated by the difference in the integrals of the two peaks. Indeed, the mean cranial capacity falls within the second peak of the distribution (male peak) and not in between the two peaks, as it should happen for a balanced sex representation of endocranial volumes (see Supplementary Materials for more details). Therefore, this subset of data should be eliminated by the whole (DeSilva et al, 2023) dataset because the overall available data of *H. sapiens*' endocranial volumes for age >1 ka is of only N = 278 individuals, and a subset of N = 25 of sex-representation unbalanced data is approximately 9% of the total, a too high percentage of the whole dataset, causing strong bias in any further analysis of the time evolution of the endocranial volume.

3 Was there an endocranial volume reduction during the end of the Holocene?

By means of the histogram analysis of Supplementary Figure S4, it has been shown that at least one subset of data—N=25 data corresponding to the age=11.5ka of the whole dataset (DeSilva et al., 2023)—used for the changepoints search was strongly biased towards male endocranial volumes. Therefore, this biased subset of data must be discarded as a not-representative value of endocranial volumes. If this sex-representation unbalanced subset of data is eliminated, the mean for the 11.7 ka ≥ age > 5 ka interval changes remarkably, as it has been shown by the red square in Supplementary Figure S2. The elimination of this subset of data affects time-evolution analysis of the endocranial volume, questioning if the changepoint of DeSilva et al. (2021, 2023) for an age of 3–5 ka is reliable.

Supplementary Figure S5 shows the histogram for the N=72 endocranial volumes of *H. sapiens* reported by DeSilva et al. (2023), for the 5 ka ≥ age > 0.15 ka interval. The dashed line indicates the mean cranial capacity, which falls at the end of the first main peak of the histogram. This subset of data is slightly biased towards female endocranial volumes, as it can be estimated by the difference in the integrals of the two peaks of the distribution. Therefore, the actual average cranial capacity for the 5 ka ≥ age > 0.15 ka interval should be also slightly greater than the value of 1,389 cc obtained averaging these N=72 data. In any case, if we calculate the difference between the mean of these 72 individuals corresponding to the 5 ka ≥ age > 0.15 ka interval, with respect to the mean at an age of 0.1 ka, we obtain $t = (1,389 - 1,341)/(130/\sqrt{72}) = 3.13$ and $p < 0.0015$. Thus, the reduction in the endocranial volume in the period 5 ka ≥ age > 0.15 ka should be considered as a reliable conclusion. A better sex-balanced 5 ka ≥ age > 0.15 ka dataset would have given a still lower value of p. Thus, the above analysis confirms the result of DeSilva et al. (2021, 2023) of an endocranial volume reduction during the last 3–5 ka and discussed by several other authors (von Bonin, 1934; Tobias, 1970; Schwidetzky, 1976; Wiercinski, 1979; Beals et al., 1984; Henneberg, 1988, 1998, 2004; Brown, 1992; Henneberg and Steyn, 1993, 1995; Ruff et al., 1997; Brown and Maeda, 2004; Wu et al., 2007; Bailey and Geary, 2009; Hawks, 2011; Balzeau et al., 2013; Bednarik, 2014; Liu et al., 2014; Stibel, 2021, 2023; Wu et al., 2022).

4 Is the endocranial volume reduction characterizing all *Homo sapiens* evolution?

Figure 1 shows the mean endocranial volumes versus mean ages for the following: *H. sapiens* (black); *H. neanderthalensis* (red); *H. heidelbergensis* (blue); *H. erectus* (dark yellow); *H. habilis* and *H. rudolfensis* (magenta); *Rudapithecus*, *Sahelanthropus*, *Ardipithecus*, and *Australopithecines* (green). Data have been taken by DeSilva et al. (2023). The mean values shown in Figure 1 have been reported in Table 1.

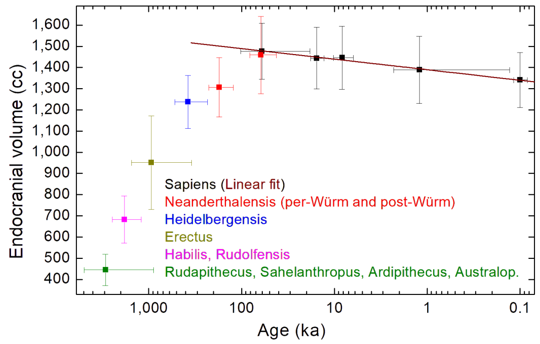

FIGURE 1
Mean endocranial volumes versus mean ages for *H. sapiens* (black); *H. neanderthalensis* (red); *H. heidelbergensis* (blue); *H. erectus* (dark yellow); *H. habilis* and *H. rudolfensis* (magenta); *Rudapithecus, Sahelanthropus, Ardipithecus, and Australopithecines* (green). Data taken by (DeSilva et al., 2023). The brown line is a linear fit of the *H. sapiens*' mean data reported in Table 1.

The mean values plotted in Figure 1 shows that the mean endocranial volumes of hominids non-*Homo*, and of *H. habilis*, *H. rudolfensis*, and *H. erectus* are, in a Log(age)-scale, aligned along a nearly linear growth. The same happens for *H. heidelbergensis*, pre-Würm *H. neanderthalensis*, and post-Würm *H. neanderthalensis*, although the slope of the nearly linear growth evidently changes. The brown line plotted in Figure 1 is a linear regression of the endocranial volumes versus log values of the age, reported in Table 1 for *H. sapiens*, after having discarded the male-biased 11.5 ka subset of data, as already discussed. The linear fit for the Cranial Capacity (CC) gives the following time dependence:

$$CC = 1,240.8 \pm 12.8 + (49.7 \pm 3.4) \times \mathrm{Log(age)} \qquad (1)$$

with the age expressed in years and the cranial capacity expressed in cc.

In the above linear fit, we have considered mean values for avoiding the time unbalance of data towards more recent ages because reducing data to means is a standard practice in timeseries analysis calculated to represent specific temporal slices (Auger and Lawrence, 1989; Wagner et al., 2002; Villmoare and Grabowski, 2022). Supplementary Figure S6 shows details of the fit. All experimental points fall within the 95% interval of confidence if we neglect the data at 11.5 ka. The adjusted R-square is 0.98, showing that these mean values follow just a linear regression as a function of the Log(age).

If we calculate a linear regression of all data for *H. sapiens* reported by DeSilva et al. (2023) in the range 300 ka ≥ age > 0.1 ka, substituting only their data for the age ~1 ka with the mean value of 1,431cc (N=10,363), without performing any averaging of data, the following linear regression is obtained:

$$CC = 1,236.2 \pm 53.6 + (53.7 \pm 13.5) \times \mathrm{Log(age)} \qquad (2)$$

In this last linear regression, the adjusted R-square is only 0.05, indicating that the origin of the high variance of data, with respect to the model, cannot be explained by the endocranial volume reduction as a function of Log(age). Indeed, the origin of the high variance of data is related to the high variability of cranial capacity of *H. sapiens*, which spans a 1,000 cc range (Holloway et al., 2004), together with the very low number of fossils available for different ages. From the linear regression, we have a reduction of approximately 50 cc for each log-decade (Equations 1, 2); 50 divided 1,000 is just 0.05, the adjusted R-square value. Therefore, due to the paucity of fossils, 95% of the variance of data of (DeSilva et al., 2023) is related to the high variability of *H. sapiens*' endocranial volumes, only 5% to time evolution.

There is also another reason that affects this high variance of data. Indeed, the natural logarithm of endocranial volumes versus the natural logarithm of age has been recently shown also in Wu et al. (2022; see Figure 7 therein) for datasets published in Holloway et al. (2004), Li et al. (2017), and Ni et al. (2021). An overall increasing cranial capacity is evident, excepted in the late Pleistocene period, so confirming a period of negative rate change in *H. sapiens*' endocranial-volume evolution. However, there are

TABLE 1 Mean endocranial volumes and mean ages averaging data taken from (DeSilva et al., 2023).

Species	Rudapith., Sahelanth., Ardipith., Australop.	Habilis and Rudolfensis	Erectus	Heidelberg.	Neanderth. post-Würm	Neanderth. pre-Würm
N	34	8	48	26	14	12
Average endocranial volume (cc)	445±74	683±111	951±221	1,237.5±125	1,459±182	1,306±140
Average age (ka)	2,926±2,040	1,833.8±633	937±593	378±144	61.8±19.6	173.9±51.1
Species Time Intervals (ka)	**Sapiens 300≥age>23.4**	**Sapiens 23.4≥age>11.7**	**Sapiens 11.7≥age>5**	**Sapiens 11.7≥age>5 (**)**	**Sapiens 5≥age>0.1**	**Sapiens age∼0.1**
Number of data (N)	62	74	68	43	72	10,363 (*)
Average endocranial volume (cc)	1,477±132	1,444±132	1,481±161	1,446±149	1,389±158	1,341 ± 130
Average age (ka)	60.4±61.2	15.5±2.6	9.44±2.23	8.24±1.98	1.21±1.08	0.1

(*) Value obtained averaging data taken from different sources (see main text for details).
(**) Without N=25 data for age=11.5ka, of fossils found at Afalou, Algeria (Vallois and Hallam, 1952).

also important exceptions to the general trend: we have found species with very low cranial capacity (*Homo floresiensis*, *Homo luzonensis*, and *Homo naledi*) compared to average *H. sapiens*' endocranial volumes; moreover, there is the earliest evidence of a 200–160 ka hominin (XJY6 fossil) with brain size in the upper range of *H. neanderthalensis*' and modern *H. sapiens*' values (Wu et al., 2022). All these findings imply a dependence of the cranial capacity not only on time but also on the geographical region, contributing further to the big variance of data.

5 Discussion

If data of different species are merged, as done in the last linear regression reported in the Supplementary Materials, the main characteristic of the *H. sapiens*' evolution is lost: a gradual and continuous decrease in the endocranial volume from the origin of the species, set 300 ka ago according to the oldest fossils, until now. Some studies have placed the beginning of the cranial capacity reduction in the late Pleistocene (approximately 35 ka) (Ruff et al., 1997) and others in the more recent Holocene (about 10 ka) (Henneberg, 1988; Hawks, 2011). Instead, the linear fit of Figure 1 indicates that endocranial volume reduction of *H. sapiens* is not a characteristic only of the last 3–5 ka, but it is going on at least from the late Pleistocene, as suggested in (Ruff et al., 1997), and probably from the beginning, from the oldest fossils' age (300 ka). Figure 1 shows that different species have different processes of endocranial volume increase/decrease (Bruner, 2017). In particular, the evolution of *H. sapiens*' endocranial volume seems to be in countertrend to the overall increase common to other hominid/hominin species, if we discard few exceptions, related to the small-brained Middle and Late Pleistocene hominins *Homo naledi* (Berger et al., 2015; Montgomery, 2018) and *Homo floresiensis* (Brown et al., 2004b). *Homo neanderthalensis* is characterized by a time increment of the average endocranial volume, which reaches the *H. sapiens*' value when interbreeding of the two species has, probably, become more pronounced (Gokcumen, 2020), as shown by the pre-Würm and post-Würm mean values plotted in Figure 1, with the post-Würm value for *Homo neanderthalensis* very close to the *H. sapiens*' value of the same age.

Figure 1 shows that *H. sapiens*' evolution seems to be an exception, because its mean cranial capacity has been decreasing as a function of time, from the oldest age of the first fossils found. This finding could imply that *H. sapiens*' origin might be related to more ancient hominid species than those until now discovered. Future work could aim to extend the analysis of DeSilva et al. (2023) also to other dataset not considered in their work, such as the dataset reported in (Stanyon et al., 1993). Also the analysis of brain weights normalized to the body weight (Nooranipour and Farahani, 2008), for fossils for which this is possible, could allow to obtain new insights on endocranial volume time evolution. In any case, future discoveries of new fossils, particularly of very ancient *Homo-sapiens*' fossils (perhaps also for age >300 ka), and new genetic studies of the archaic interbreeding of hominins (Rogers et al., 2020; Bergström et al., 2021), should allow to better understand the origin of our species and its endocranial volume evolution.

Author contributions

LD: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1368347/full#supplementary-material

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