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**Natahi, Sélim, Neubauer, Simon, Tsegai, Zewdi J., Hublin, Jean-Jacques and Gunz, Philipp (2022) *Covariation of endocranial shape and cranial vault thickness in present-day humans and Neandertals*. In: *PaleoAnthropology. 12th Annual Meeting of the European Society for the Study of Human Evolution Abstracts*. 2022 (2). p. 548. Paleoanthropology Society**

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Poster Presentation Number 40, Session 1, Thursday 18:15

## Covariation of endocranial shape and cranial vault thickness in present-day humans and Neandertals

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A better understanding of the patterns of brain growth and development in extinct but also in extant great apes informs discussions about the evolution of cognitive abilities and behaviors in the human lineage. In fossils, brain shape and its cortical organization can usually only be inferred from the shape of the endocranial cavity and from the brain imprints in the cranial bone. However, the shape of the braincase results from different mechanisms: the patterns of brain growth and development [1], the evolutionary and developmental changes affecting facial size and shape [2], the development of soft tissues [3] and the pattern of growth and development of the entire neurocranium [4]. It has been shown that present-day humans and Neandertals achieved similar endocranial capacities via different developmental pathways, suggesting underlying differences in the tempo and mode of brain growth and development [5].

Here, we assess the influence of bone thickness on endocranial shape. Specifically, we examined to what extent differences in bone thickness of the cranial vault can explain the endocranial shape differences between present-day humans and Neandertals. Our sample comprises 75 computed tomographic scans of adult present-day humans and 6 Neandertals. Endocranial shape was measured using 935 landmarks and semilandmarks and analyzed after a Procrustes registration. Cranial vault thickness (CVT) was computed from 472 landmarks and semilandmarks as the distance between the endocranial and the ectocranial surfaces. We first quantified CVT standardized for the size. Second, we explored the covariation between endocranial shape and the cranial vault thickness using a two-blocks partial least-squares analysis (PLS). Last, we established a predictive regression model of endocranial shape using cranial thickness as an input variable and endocranial shape as an output. We built this model from the present-day human sample only, and measured the fitness of the model in explaining the endocranial shape that characterizes the Neandertal individuals.

Our results demonstrate that even though Neandertals tend to have a thicker cranial vault, these values are still comprised within the range of variation of present-day humans. The first dimension of covariation in the PLS analysis was driven by variation within present-day humans. Individuals displaying elongated shapes showed an overall thinner CVT, while those with rounded vaults had a thicker cranial vault. Scores along the second axis of covariation displayed a shift between present-day humans and Neandertals. Along this axis, present-day humans were characterized by bulged, vertically stretched and thin parietal bones, while Neandertals displayed vertically shorter, wider and thicker parietal bones. Finally, our regression model failed to predict the Neandertal endocranial shape from their CVT values. Altogether, our results suggest that endocranial shape differences between present-day humans and Neandertals are not likely to be explained by their CVT, and strengthen the hypothesis of different brain shapes between these two human groups.

We are thankful to all curators and technicians for access to and CT scanning of fossils and present-day humans. We acknowledge the Fyssen foundation and the Max Planck Society for funding. This research was supported by Marie Skłodowska-Curie Grant #101025719 (ZJT).

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