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Model-based inferring of Neanderthal upper cervical spine motion

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Summary - *The primary aim of this pilot study is not to provide definitive statements on Neanderthal kinematics, but rather to illustrate the potential of Procrustes Motion Analysis (PMA) combined with predictive modelling as a robust tool for addressing questions of functional morphology in the fossil record. We use this novel approach to model and compare the potential upper cervical spine (UCS) flexion-extension kinematics of the La Ferrassie 1 Neanderthal and modern humans. The study material comprised the 3D virtual morphology of the occipital base, atlas (C1), and axis (C2) of La Ferrassie 1 and the corresponding kinematic and morphological data from seven unembalmed modern human cadaveric specimens. We first used the PMA framework to analyze the shape-motion relationship in the modern human sample. This relationship was then used to build a predictive model. We applied this model to the UCS morphology of La Ferrassie 1—inferring its potential motion trajectory rather than measuring direct fossil kinematics—and statistically compared the results to the modern human mean. Contrary to previous hypotheses based solely on morphological inference, our model-based results challenge the assumption of reduced Neanderthal neck mobility. The inferred trajectory of flexion-extension for La Ferrassie 1 were statistically comparable to that of the modern human sample, suggesting no significant difference in this specific movement. This study demonstrates the utility of integrating empirical motion data, geometric morphometrics, and predictive modelling in paleoanthropology, offering a significant advance over traditional morphological inference. By successfully illustrating the application of PMA, this research provides a new framework for investigating hominin kinematics, while simultaneously emphasizing that the kinematics presented for the Neanderthal specimen were predicted and modelled, not directly measured.*

Keywords - *Neck, Mobility, Flexion-extension, Range of motion, Neanderthal.*

Introduction

The big picture in human evolution is most often related to paleoecology and fossil hominins behavior, such as cannibalism (Villa et al. 1986; Goldberg 1997; Fernández-Jalvo et al. 1999; Vilaca 2000; Saladié et al. 2012), sick care (Kessler et al. 2017, 2018; Kessler 2020), child care (Gettler 2010; Kramer and Otárola-Castillo 2015; Halcrow et al. 2020), use of fire (Sandgathe 2017; Brittingham et al. 2019), hunting (Bunn and Pickering 2010; Kübler et al. 2015; Bartolini-Lucenti et al. 2021) or locomotion patterns (Harcourt-Smith and Aiello 2004; Crompton et al. 2008; Raichlen et al. 2011; Stewart et al. 2019). Inherent in any kind of behavior is the concept of motion. Even behaviors that may seem less obviously related to movement —such as caregiving or cannibalism— require specific bodily actions, including transport, manipulation, or postural adjustments, which are constrained by anatomical and biomechanical capabilities. As Tinbergen clearly stated: behavioral repertoires are the "total of movements made by the intact animal" (Tinbergen, 1951, p.2); therefore, quantitative analyses that enable statistical comparisons of motion are crucial to any study aiming to understand behavior and hominin evolution.

In the past, possible neck kinematic differences between hominin species have been addressed mainly through the inference and interpretation of morphological characters, such as the location of ligament or muscle insertions and the robusticity of specific osteological features (Gómez-Olivencia et al. 2013). Later, with the expansion of geometric morphometrics, the entire morphology and spatial relations of the bones began to gain importance in the analysis of morpho-functionality (Palancar et al. 2020b) C1. Nowadays, more exhaustive analyses are using empirical motion data to address variations in hominins kinematics (Palancar et al. 2024; Taverne et al. 2024). Procrustes Motion Analysis (PMA) represents a robust method that combines geometric morphometrics with real motion data (Adams and Cerney 2007), and opens the way for future developments of morpho-functional studies related to hominin evolution.

During the last two decades of the twentieth century, human motion analysis gained significant attention from researchers (Aggarwal and Cai 1999). Most of the studies carried out during those years were focused on one of the three areas related to motion analysis defined by Aggarwal and Cai (1998): (1) body structure and joint analysis, (2) tracking moving individuals or (3) recognition of human movements. Quantitative analyses of motion using geometric methods were not developed until the early 21st century (Slice 2007). PMA was the first approach to functional analysis of motion and quantification of motion patterns through geometric morphometric techniques (Adams and Cerney, 2007). PMA unifies the three areas described by Aggarwal and Cai (1998) as it analyzes the posture shapes (1, body analysis), the changes in posture from one time step to another (2, tracking) and the trajectory of motion (3, pattern recognition of movements), while also adding the possibility for statistical comparisons of the latter. PMA is based on the principle that "any motion can be represented by an ordered sequence of postures exhibited throughout the course of a motion" (Adams and Cerney 2007, p.438). This approach –or similar ones– has been applied to the study of feeding motion in fishes (Martinez et al. 2018), the ventricular heart cycle (Piras et al. 2014), the gait of scorpions (Telheiro et al. 2021) or even human gait (Waldock et al. 2016) and breathing patterns (Gómez-Recio et al. 2024). These studies have shown that the shape of landmark configurations assigned to different postures of a motion trace a trajectory through morphospace (Gerber 2017) that quantifies the motion itself and identifies differences between individuals or groups. Despite its potential in analyzing different motion patterns during human evolution, PMA has not yet been applied in a paleoanthropological context.

Cervical spine morpho-functionality

The cervical spine is an important region of the vertebral column that supports the head, protects the upper spinal cord and is the attachment site of various muscles involved in the kinematics of the upper limbs, thorax and head (White and Panjabi 1990). The cervical spine is usually described in two regions that can be differentiated developmentally, anatomically and functionally (White and Panjabi 1990): the upper cervical spine (UCS) combining the occipital atlantoaxial complex (i.e. occiput C0, atlas C1, axis C2)(Bernard et al. 2015) and lower cervical spine (i.e. C3 to C7). The lower cervical spine, which connects with the thorax, consists of five subaxial cervical vertebrae that show the typical cervical morphology (i.e. small vertebral body, uncinate processes, a triangular shape of the neural canal and transverse foramina) (White and Panjabi 1990). Superiorly, the two remaining vertebrae of the UCS, atlas and axis, show a particular anatomy. The atlas lacks the vertebral body, substituted by the dens of axis, and does not present a spinous process. Additionally, the articular facets display specific shapes and orientations compared to the subaxial cervical vertebrae. Developmentally, there are three modules: superior (C1-C2), middle (C3-C5) and inferior (C6-C7), that have their embryonic origin in the somites and are regulated by Hox genes (Arnold et al. 2017; Randau et al. 2017). The cranial base is also derived from the somites and regulated by the Hox1 gene and thus, it was proposed to be part of the superior module (Arnold et al. 2017; Randau et al. 2017; Villamil 2018). Functionally, two complexes can be differentiated: the superior one, formed by the occipital condyles, atlas, and axis, where rotation is the principal motion; and the inferior one, formed by the subaxial cervical vertebrae, where lateral bending and flexion-extension are more determinant (White and Panjabi 1990). Thus, the upper cervical spine is a singular complex that can be isolated from the rest of the column to perform exhaustive analyses on it, due to its particular conditions: anatomy and function.

During the last decade, several works have increased the knowledge on the variability, allometry and integration patterns of the hominid cervical vertebrae (Gómez-Olivencia et al. 2013; Arlegi et al. 2018; Meyer et al. 2018; Villamil 2018; Palancar et al. 2020a,b). Specifically, Neanderthal cervical vertebrae present several differences compared with modern humans, such as a greater mediolateral width and dorsoventral diameter, as well as longer and more horizontally oriented spinous processes (Gómez-Olivencia et al. 2013). These anatomical differences led several authors to propose functional implications for the Neanderthal cervical spine: less lordosis and more stability, compared with *H. sapiens* (Gómez-Olivencia et al. 2013; Been et al. 2017). However, these hypotheses were based on clinical studies performed on a modern human sample and no experimental data had been tested (Mayoux-Benhamou et al. 1994; Olson et al. 2006; Alpayci et al. 2016; Been and Bailey 2019).

Focusing on the morpho-functionality of the cervical spine, Manfreda et al. (2006) and Nalley and Grider-Potter (2015, 2017) found various vertebral measurements related to posture or locomotor patterns in Primates, confirming the existence of a morpho-functional relation in the Order (Manfreda et al. 2006; Nalley and Grider-Potter 2015, 2017). Even so, no motion data had been analyzed until more recently (Grider-Potter et al. 2020; Palancar et al. 2024; Taverne et al. 2024). Measuring ranges of motion of several species of Primates and testing its relation with vertebral shape variables, Grider-Potter et al. (2020) found no association between vertebral shape and mobility. In contrast, Palancar et al. (2024) found a possible positive morpho-functional relation in a modern human sample in both rotation and flexion-extension movements of the atlas vertebra. In the latter work, they also estimated the ranges of motion of several Neanderthal atlases, based on the human positive relation. Contrary to previous hypotheses on Neanderthal cervical spine mobility, they concluded that no differences were observed between Neanderthals and modern humans ranges of motion of the atlas (Palancar et al. 2024).

However, analyzing ranges of motion considers only the maximal capability but not the way it is actually acquired, which is the spatio-temporal trajectory pattern. It is possible that modern humans and Neanderthals may well have had similar flexion-extension range of motion but different spatio-temporal trajectory patterns. The aim of the present work was therefore to apply for the first time Procrustes Motion Analysis (PMA) methods in a paleoanthropological context, to estimate the UCS motion behavior of La Ferrassie 1 and to assess possible differences between this Neanderthal and modern humans in terms of mobility.

Material and methods

Material

The modern human sample consists of seven unembalmed human specimens analyzed in previous works (Beyer et al. 2020; Palancar et al. 2024), in which dissections involved removing the superficial soft tissues to access the upper cervical spine and its associated anatomical structures such as ligaments, suboccipital muscles, and fascia. All these structures were kept intact, while the lower cervical segment (below the third cervical vertebra), mandible and anterior viscera of the neck were removed. Descriptions of specimen preparation and 3D model extractions can be found elsewhere (Dugailly et al. 2010, 2011, 2013). The modern human individuals were aged

65 to 80 years and showed no cervical trauma or history of spine surgery. They exhibited arthrosis but showed no significant degenerative processes in the upper cervical spine; the most pronounced issues were found in the lower cervical spine, as detected by Tao et al. (2021). Individuals with fractures, exostosis, or anatomical variants were excluded. In the sample, lordosis of the UCS ranges between 27° (minimum) and 37.3° (maximum), with a mean of 31.3°.

The fossil sample consists of the skull, atlas and axis of La Ferrassie 1, a Neanderthal individual found at the La Ferrassie site, located in Dordogne (France), and dated to 43-45 ka (Heim 1976; Guérin et al. 2015; Gómez-Olivencia et al. 2018). These fossils show some damage that required reconstruction/estimation to be used in this study. In the case of the atlas, La Ferrassie 1 lacks the left transverse process. As the transverse foramen is not analyzed here, only the landmark on the most lateral point of the transverse process had to be estimated, in this case by mirror imaging. The axis does not preserve three landmarks: the tip of the dens and both transverse processes. Those were estimated by thin-plate-spline (TPS) interpolation using the function *estimate missing* from the geomorph package version 4.0.5 (Adams and Otárola-Castillo 2013) in RStudio. Regarding the occipital base, only one landmark in the mastoid sulcus had to be estimated, by mirror imaging.

Kinematic data

Motion data of the skull, atlas and axis in both flexion-extension and axial rotation were obtained from previous work (Dugailly et al. 2010; Beyer et al. 2020). Each anatomical preparation was set on a custom-made jig with the skull oriented downward and fixed to a rigid plate. The Frankfurt plane of the head (the plane between the upper border of the external auditory meatus and the margo infraorbitalis) was aligned with the horizontal plane. Passive motions of cervical vertebrae were applied using two metallic pins rigidly screwed into C3 (one vertical pin through C3 body, one pin in C3 transverse processes). The latter provided a fully free spatial displacement of C2 during the procedure by avoiding potential constraints at the pin–bone interface. During data collection, the vertebrae were moved by displacing the pin in two different planes of interest separately in several steps. Kinematics were analyzed from five sagittal discrete positions during two different motions:

- Flexion-extension: from neutral to intermediate and maximal flexion and extension.
- Rotation: from neutral to intermediate and maximal right and left rotation.

At each discrete position, spatial locations of the bones were recorded using a 3D-digitizer (FARO, B06/Rev 18), pointing technical markers previously added to the bones (Dugailly et al. 2010). The output of discrete joint displacements was processed using a standard mathematical method for motion kinematic computation (Cappozzo et al. 1995). Details about the entire experimental set-up and validation protocol can be found elsewhere (Dugailly et al. 2010, 2011, 2013; Beyer et al. 2020).

Motion analysis

Each anatomical preparation was scanned in neutral position using computed tomography (Siemens SOMATOM, helical mode, reconstruction: slice thickness = 0.5 mm, inter-slice spacing = 1.0 mm, image data format = DICOM). Segmentation and 3D model reconstruction were performed using semi-automatic procedures on the software Amira version 5.4.0 (Visage Imaging, Inc.) to obtain the surface of the bones and no viscera.

A total of 236 shape (semi)landmarks were placed on each individual following the digitization template of high-density geometric morphometrics of occipital base (Palancar 2023) (Fig. S1, Tab. S1), atlas (Palancar et al. 2020b)C1 (Fig. S2, Tab. S2) and axis (Palancar et al. 2021) (Fig. S2, Tab. S3). Then, in software lhpFusionbox (Chapman et al. 2013) kinematic data obtained on the experiment via the technical markers were applied to the shape (semi) landmarks to obtain the upper cervical spine shape of the individual on each of the discrete positions.

Then, motion trajectories were obtained by applying the protocols detailed in Waldock et al. (2016).

1) Firstly, we performed a Procrustes registration without scaling (in order to control for scale during the third step) of the entire sample to translate and rotate each posture of each individual to a common centroid.
2) Secondly, we standardized the sample by shape extraction of the motion residuals: i.e., we subtracted the individual mean from each of the postures of the individual.
3) Thirdly, we standardized size: these motion residuals are scaled by the ratio of the centroid size of the individual mean to the sample mean. This way we scale the motion residuals proportionally to the entire sample size.
4) Finally, we performed a Principal Component Analysis (PCA) on the scaled motion residuals that represents the trajectory of the motion itself. These analyses are performed on each motion direction (flexion-extension and rotation) separately.

Shape vs. motion

To test whether there is a relation between the shape of the UCS and the trajectories of the motion we performed different two-block Partial Least Squares analyses (2B-PLS) using function pls2B in RStudio v. 2023.03.0+386, package Morpho 2.5.1 (Schlager 2017), one for flexion-extension and one for rotation. The p-value of the 2B-PLS is determined by permutation testing (1000 permutations) (Schlager 2017). The shape of the UCS is considered as the individual mean of the five discrete positions measured in each motion, which we refer to as the *mean position*. The motion trajectories are considered as the PC scores from the PCA that collectively explain more than 95% of variation (Fig. 1).

La Ferrassie 1 estimation

Since the fossil bones of La Ferrassie 1 individual were isolated, we first had to articulate them to obtain the *mean position* of the UCS of this Neanderthal. For that, we used the function rotonto in RStudio v. 2023.03.0+386, package Morpho 2.5.1 (Schlager 2017) to rotate and translate each bone separately to the modern human mean configuration. Once we obtained the *mean position* of La Ferrassie 1, we predicted through the PLS analysis, the motion trajectory of this Neanderthal: the PC scores. We did that by using the previous 2B-PLS, using the function predict PLS from Data (package Morpho 2.5.1; Schlager 2017). The predicted motion trajectory of La Ferrassie 1 is statistically compared with the modern humans by a permutation test using the permudist function (package Morpho 2.5.1; Schlager 2017). To assess the reliability of the results, we performed a leave-one-out cross-validation within the modern human sample (argument “cv” of the function pls2B). By using the shape predictor function in package geomorph 4.0.4 (Baken et al. 2021) we extracted the motion residuals and added them to the *mean position* of La Ferrassie 1 to see the five estimated discrete positions. Finally, to facilitate the visualization and interpretation of the results, cubic-spline interpolation of the landmarks trajectories were estimated using the function interp1 in MATLAB v. 9.7.0. (MATLAB 2018): several intermediate positions were estimated resulting in a total of 50 postures. These kinematic data were then fused with the 3D model using lhpFusionbox software to further visualize the motion in 4D format.

Results

The PCAs performed on the motion residuals that represent the flexion-extension and rotation motion trajectories are shown in Figure 1. In the flexion-extension motion (Fig. 1A), the first three PCs explained more than 95% of the variability and were significantly related via PLS with the *mean position* of the UCS (87% correlation, p-value < 0.1). The result of the leave-one-out validation can be found in Supplementary Online Material (Fig. S3). In the rotation motion

(Fig. 1B), the first five PCs explained more than 95% of the variability but were not related significantly via PLS with the *mean position* of the UCS (p-value = 0.261).

The *mean position* of La Ferrassie 1, obtained from the rotation and translation of each isolated bone to the modern human mean position, is shown in Figure 2. Based on this *mean position* of La Ferrassie 1 - and the positive relation found for flexion-extension motion between *mean position* and motion trajectory - we obtained the five estimated postures of this specimen during flexion-extension (Fig. 3). By interpolating intermediate postures, we created a video of the flexion-extension motion of the UCS of La Ferrassie 1 (compared to a modern human) (electronic supplementary material, video SV). The permutation test comparing the Neanderthal and the modern human mean was not statistically significant (p-value = 0.9, PD = 8.65).

Although not statistically significant, Figure 3 and the video indicate that, compared to modern humans, in maximal flexion, the skull of La Ferrassie 1 points more inferiorly and, in maximal extension, more superiorly. The plot of the video indicates the length variation between the Inion and the spinous process of C2 during motion. It is seen that, although similar and almost parallel, the curves differ slightly and show that the increase in length is greater in La Ferrassie 1. Table S4 shows the distance between Inion and C2 spinous process during time of both La Ferrassie 1 and the modern human mean. As shown in Table S4, although there is also more extension, it is during the flexion where La Ferrassie 1 exhibits the greatest motion.

Additionally, in maximal extension (Figure 3A), the spinous processes of La Ferrassie 1 do not serve as a physical limit to the motion as they are not yet in contact. However, in the modern humans mean, the atlas and axis processes touch each other in this position, thereby limiting this motion.

Discussion

Motion analysis is a key element linking anatomy, biomechanics, and a wide range of behaviors that can be statistically interpreted in wider paleoecological frameworks. Consequently, any methodological development in this domain is of potential importance in paleobiology. Here, we developed virtual methods to apply specific aspects of arthrokinematics within the framework of geometric morphometrics. For the first time, PMA has been applied in a paleoanthropological context. Thanks to this method, it was possible to establish relevant predictions not only about its range of motion but also about how La Ferrassie 1 Neanderthal would have flexed and extended the UCS. Our findings highlight the potential of integrating motion capture with geometric morphometrics techniques to investigate functional anatomical problems and patterns of movement in human evolution.

Neanderthal cervical mobility

The first comprehensive analysis of the Neanderthal cervical vertebrae was carried out by Gómez-Olivencia et al. (2013). In that study, the authors suggested that certain morphological features—specifically the longer spinous processes in the mid-cervical region (particularly C5–C6)—could have made neck extension more difficult in Neanderthals. They proposed that achieving a range of motion comparable to that of modern humans might have required a less lordotic cervical spine. However, more recently, Palancar et al. (2025) have reinterpreted the Neanderthal cervical spine as exhibiting similar —or even greater— cervical lordosis compared to modern humans. Even so, Gómez-Olivencia et al. (2013) also noted that the more horizontal orientation of the spinous processes may have acted as a compensatory mechanism, potentially allowing for greater extension of the cervical spine. On the other hand, Been and Bailey (2019) more explicitly hypothesized reduced cervical mobility in Neanderthals, based on a combination of morphological features and clinical extrapolations. More recently and basing the interpretation on experimental data obtained in modern humans, Palancar et al. (2024) suggested that the Neanderthal atlas (C1) would have similar ranges of motion to *H. sapiens*

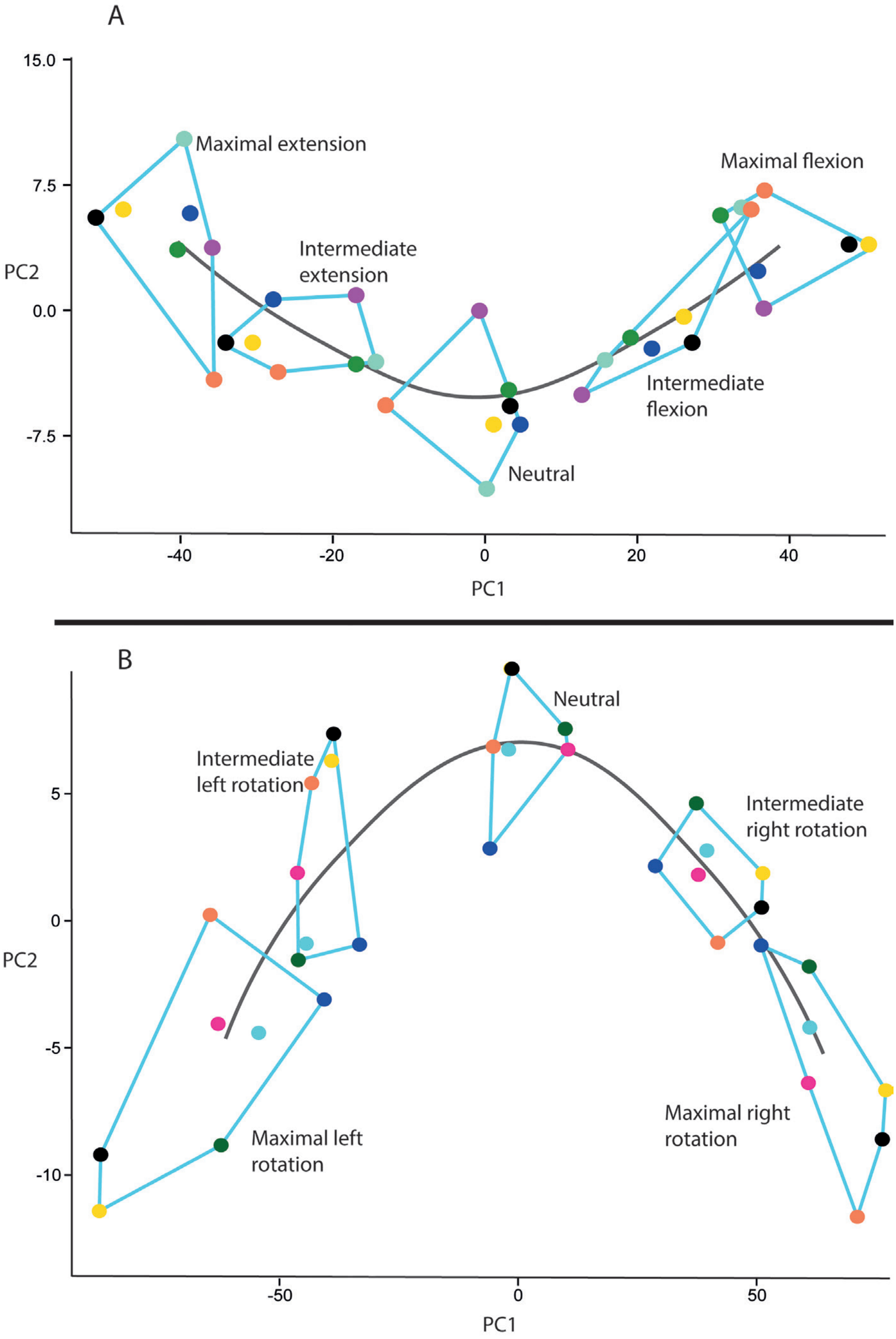

***Fig. 1** - Principal Component Analysis plots of the scaled motion residuals. The curved line draws the mean motion trajectory in flexion-extension (A) and rotation (B). Convex hulls group all the individuals in each of the five discrete positions.*

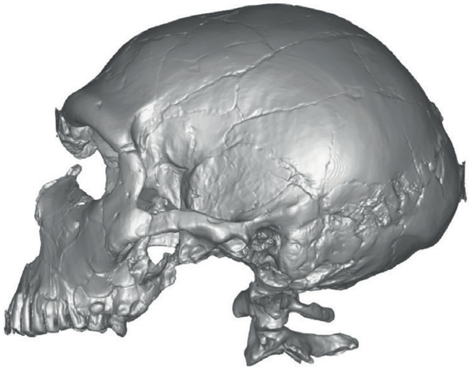

Fig. 2 - **Mean position of La Ferrassie 1 individual, obtained as the result of the translation and rotation of each isolated bone to the mean position of the modern human sample.**

in both axial rotation and flexion-extension. Here, by increasing the study area to the entire UCS, we obtained a predicted flexion-extension motion for the Neanderthal of La Ferrassie 1 that could be similar to that of modern humans. Both Palancar et al. (2024) and the present work suggest that the question of Neanderthal neck mobility should be revisited. Moreover, cervical spine mobility and its musculo-skeletal configuration are not only related to neck flexion-extension or basic movements, but also to upper limb mobility and the stabilization of the head during walking and running. For example, the great apes possess an *atlanto-clavicularis* muscle, which is attached to the transverse processes of atlas and the clavicle, and acts during elbow extension in quadrupedal locomotion (Aiello and Dean 1990). Regarding the stabilization of the head, recently Yegian et al. (2021) proposed that the evolution of long-distance running may have favored the reduction of the rotational inertia of the head, changing its configuration and size (Yegian et al. 2021). Differences in the stabilization of the head can also be noticed in the presence of the nuchal ligament: among great apes, only hominins possess this ligament, which has evolved independently in other mammals adapted for running like dogs and horses (Bianchi 1989).

Hominin kinematics and locomotion

Another important aspect of Neanderthal anatomy related to neck and body kinematics is the semicircular canal system. Spoor et al. (2003) suggested that the relatively small vertical canals in Neanderthals implied reduced agility and a locomotor repertoire characterized more by endurance walking than by running. However, subsequent studies have offered alternative perspectives. Evidence from calcaneus anatomy and biomechanics (Raichlen et al. 2011), as well as paleoecological data (Stewart et al. 2019), supports more dynamic locomotor capacities in Neanderthals, possibly including sprinting and ambush hunting. Furthermore, Bastir et al. (2020) identified morphological similarities in thorax structure between *Homo erectus* (Nariokotome) and Neanderthals (Kebara 2), suggesting that the narrow, flat ribcage of modern humans may be a more recent evolutionary development, thereby questioning earlier assumptions about locomotor differences within the genus *Homo*. While the functional implications of vestibular anatomy remain debated, our findings indicate that Neanderthal cervical mobility was not necessarily reduced, inviting a more cautious interpretation of behavioral inferences based solely on semicircular canal morphology.

The current study demonstrates that by combining virtual morphology, geometric morphometrics and experimental data, based on actual anatomical morpho-functional relations, new insights can be gained that can help test hypotheses previously grounded in theoretical reconstructions (Spoor et al. 2003; Gómez-Olivencia et al. 2013; Been et al. 2017; Been and Bailey 2019). Consequently, it seems that more exhaustive analyses point to a functionality that contrasts with the hypothesized, less mobile cervical vertebrae of this species.

Study limitations

As the PLS analysis relates the motion trajectory to the UCS mean posture, the latter shape variable is crucial. In this study, the mean posture of La Ferrassie 1 UCS is based on the modern human sample. The choice may introduce

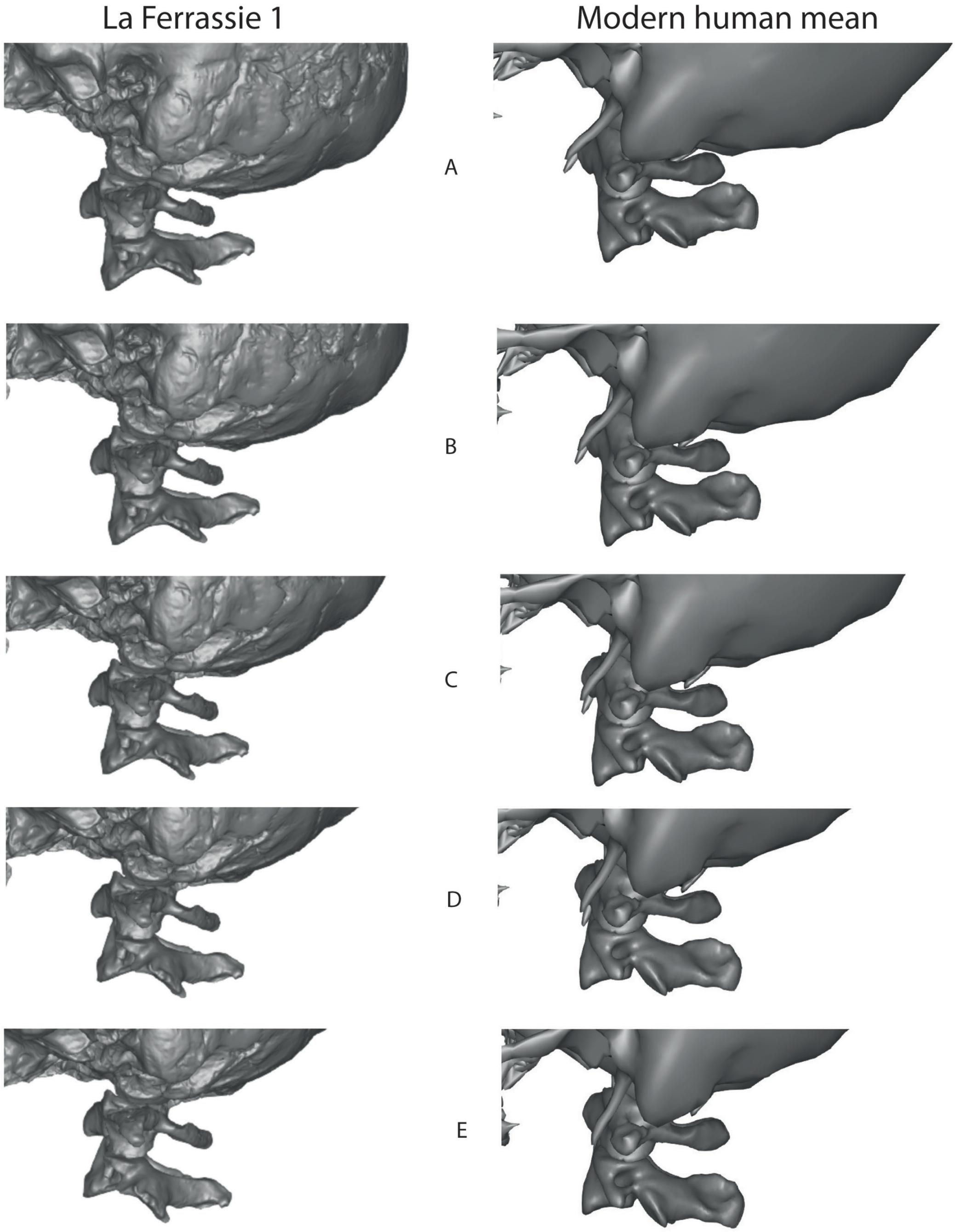

***Fig. 3** - Estimated positions during flexion-extension motion of La Ferrassie 1 (left) and the modern human mean for comparison (right). A: maximal extension; B: intermediate extension; C: neutral position; D: intermediate flexion; E: maximal flexion.*

bias, as Neanderthal cervical lordosis could differ from that of modern humans. Indeed, Been et al. (2017) proposed a less lordotic cervical spine in Neanderthals, whereas Palancar et al. (2025) suggested the opposite, and Haeusler et al. (2019) found no substantial difference in the La Chapelle-aux-Saints individual. A different cervical lordosis would result in a different UCS mean posture and could therefore alter the motion trajectory. However, current evidence is contradictory—particularly for the UCS—since the possible reduced cervical lordosis proposed for Neanderthals is based on the length of the spinous processes at C5 and C6, which are less relevant for UCS curvature. For this reason, and until more precise reconstructions are available, we have adopted the most conservative and parsimonious approach: extrapolating the UCS mean posture from modern human data. We acknowledge that future studies testing alternative configurations of cervical curvature will be valuable to assess the sensitivity of our results to this assumption.

Additionally, this study has only assessed motion differences in one region of the neck of one fossil, considering only bone-to-bone interactions. Future steps in the analysis of Neanderthal neck kinematics should include the entire cervical spine and musculoskeletal modeling to understand not only the motion of the bones but the implication of ligaments and muscle actions within the context of locomotion.

The age of the sample could be seen as a significant limitation since the modern human subjects ranged between 65 and 80 years old and exhibited some minor arthrosis. However, this is in fact beneficial for our study because the fossil we are analyzing, La Ferrassie 1, is also an older individual with several pathological lesions and osteoarthritis (Gómez-Olivencia et al. 2018). At the UCS, La Ferrassie 1 has an anatomical variant of the atlas (unilateral persistent first intersegmental artery) and significant osseous remodeling in the left half of the axis (Gómez-Olivencia et al. 2018). Therefore, an older comparative sample is more suitable for our purposes.

It is important to consider how age-related changes and degenerative conditions can affect the results. Osteoarthritis, even if mild, can affect joint mobility and biomechanics, which could alter direct comparisons with La Ferrassie 1. Previous studies have shown that osteoarthritis can reduce the range of motion and alter joint loading patterns (Thorp et al. 2006; Clynes et al. 2019). Additionally, advanced age is associated with a decrease in muscle mass and strength, which can also influence movement biomechanics (Keller and Engelhardt 2013).

To address these concerns, it would be beneficial to include a control group consisting of younger, healthier individuals in future studies. This would allow for the assessment of the impact of age and degenerative conditions on the results and provide a more comprehensive comparison. Including a more diverse control group could help distinguish kinematic differences specific to advanced age and osteoarthritis from those inherent to the pathological condition of La Ferrassie 1.

In summary, while the selection of the modern sample was justified by the need to compare with the pathological condition of La Ferrassie 1, we recognize the importance of considering how age-related changes and degenerative conditions can influence the results. Including a younger and healthier control group in future studies would provide a more comprehensive and accurate assessment of kinematic variability.

Obtaining younger cadaveric samples for studies is inherently challenging due to several factors. Firstly, younger individuals are less likely to be available for donation, as the majority of cadaveric donations come from older individuals who have passed away due to natural causes or age-related conditions. This demographic trend results in a higher prevalence of elderly cadaveric samples, which often exhibit age-related characteristics and degenerative conditions. Additionally, ethical considerations and consent processes for cadaveric donations further limit the availability of younger samples. Families may be more reluctant to consent to the donation of younger individuals, especially in cases of unexpected or traumatic deaths. Consequently, researchers frequently rely on older cadaveric samples, which, while beneficial for certain comparative studies, may not fully represent the kinematic variability observed in younger populations. This limitation underscores the importance of considering age-related changes and degenerative conditions in the analysis and highlights the need for alternative approaches to obtain a more diverse sample in future studies.

We chose La Ferrassie 1 as the case study because it is, to the best of our knowledge, the only Neanderthal fossil that preserves the skull base, atlas, and axis almost completely. In the future, if more fossil individuals are recovered preserving these bones, they should also be analyzed to expand the Neanderthal comparative sample.

It is important to note that the internal validation test (leave-one-out procedure within the modern human sample) showed limited accuracy in reconstructing the motion trajectories of excluded individuals. This outcome highlights the sensitivity of the method to inter-individual variation and underscores the extent of uncertainty that accompanies predictive reconstructions, particularly when applied to morphologies that deviate substantially from the modern human range. However, the primary aim of this study is not to provide definitive statements about Neanderthal cervical spine mobility, but rather to illustrate the potential of Procrustes Motion Analysis combined with predictive modeling as a tool for addressing questions of functional morphology in the fossil record. In this sense, the limitations observed in the validation test are informative: they delineate the current scope of the approach, while at the same time pointing toward avenues for refinement, such as enlarging comparative samples or incorporating alternative modeling strategies.

Finally, sample size is a crucial limitation. However, working with human cadaveric samples is chronically affected by such difficulties because the availability of human bodies for experimental analysis is not stable and, when available, the number of cadavers is usually small. In fact, similar cadaver samples used in similar analyses are fewer than 10 (Dugailly et al. 2010; Palancar et al. 2024; Taverne et al. 2024). Even so, since "the" main objective of this work is rather to test the capacity of PMA to detect variations in the types of movement within hominins than to understand the details of Neanderthal neck mobility, we believe that the sample size is sufficient.

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Data Availability Statement

The data supporting the findings of this study may be available from the corresponding author upon reasonable request.

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