Simulation of Anterior Biting Behaviours: Surface EMG and Strain Mapping of Craniofacial Responses

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Abstract

Reconstructing the behaviours of extinct hominin species has long relied on evidence from multiple disciplines, including archaeology, dental microwear analysis, and skeletal anatomy. Within anatomical studies, variation in craniofacial form among humans and other hominins is often interpreted as reflecting differences in habitual behaviours. One proposed explanation for this variation is anterior dental loading, in which the skull is thought to have adapted to repeated or heavy forces applied to the anterior dentition during feeding or paramasticatory activities. Finite element analysis (FEA) has increasingly been used to test this hypothesis by modelling the skull's mechanical response to forces applied during anterior dental loading. However, interspecific comparisons have yet to identify any hominin species that appears particularly well adapted to such loading, raising questions about whether methodological limitations in FEA studies may have influenced these results.

This thesis investigates one such limitation: the potential role of neck musculature in counteracting head flexion during biting tasks. The first part of the research examines whether including neck muscles in FEA models influences craniofacial strain patterns, demonstrating that their inclusion substantially alters strain magnitude and distribution. The second part records *in vivo* surface electromyographic data from the neck and masticatory muscles of a modern human during anterior pulling and clenching tasks to quantify muscle activation under realistic behavioural conditions. These data confirm that the neck musculature is actively engaged during anteriorly directed loading of the dentition.

Overall, the findings highlight that finite element models used to simulate anterior dental loading, and even standard vertical biting, should incorporate neck musculature to improve their biomechanical validity and enhance the accuracy of interpretations in craniofacial functional studies.

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Finally, I would like to thank my daughter, Maya, for teaching me how to persevere and how to manage my time more efficiently.

Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as references. I confirm that this work is original and that if any passage(s) or diagram(s) have been copied from academic papers, books, the internet or any other sources these are clearly identified by the use of quotation marks and the reference(s) is fully cited. I certify that, other than where indicated, this is my own work and does not breach the regulations of the University of York regarding plagiarism or academic conduct in examinations. I have read the University of York Code of Practice on Academic Misconduct, and state that this piece of work is my own and does not contain any unacknowledged work from any other sources.

Chapter 1: Introduction

1.1 Morphological Variability and Interpreting Past Behaviours

Over the last few million years of human evolution, one of the most striking features to fascinate palaeoanthropologists has been the remarkable diversity of the craniofacial skeleton. Among fossil hominins, craniofacial features vary between species from wide, flaring zygomatic arches and pronounced sagittal crests, to robust brow ridges, retracted midfaces and even some with anterior nasal pillars (Villmoare & Kimbel., 2011). Craniofacial morphology not only reflects phylogenetic history but also offers potential insight into differences in behaviour and adaptation. Many of these anatomical traits are thought to represent structural responses to the mechanical demands of feeding and other associated behaviours (Hirst et al., 2023).

The masticatory system, which consists of the teeth, bony skeleton, muscles, and temporomandibular joint, facilitates the placement of food between the upper and lower jaws. When biting or chewing, the forces generated by the jaw muscles are transmitted through the teeth, mandible, and craniofacial skeleton, producing specific patterns of stress and strain within the skull. According to Mechanostat theory, the strains experienced by bone can initiate modelling and remodelling processes that prompts adaptation over time. Repeated exposure to particular loading behaviours could therefore influence craniofacial form, producing morphologies that reflect the habitual mechanical environment, and by extension, aspects of diet and oral loading behaviour.

To investigate these biomechanical processes, researchers have increasingly turned to finite element analysis (FEA), a technique originally developed in engineering to model how structures respond to complex loading. FEA can be used to reconstruct anatomical structures digitally, assign them appropriate material properties, load them with simulated forces which aim to replicate loading conditions, and allow detailed prediction of stress and strain across the skull including the craniofacial skeleton (Wong et al., 2011; Parashar & Sharma., 2016; Prado et al., 2016; Alizadeh et al., 2020). FEA has been widely adopted across multiple disciplines. In clinical research, it is used to simulate surgical interventions, orthodontic forces, and implant performance (Xue et al., 2024; Zhang et al., 2024). In zoological and comparative anatomy, it provides a means of testing functional hypotheses about feeding mechanics and ecological specialisation in living species (Mitchell et al., 2025). Within palaeoanthropology, the integration of three-dimensional virtual reconstructions and FEA has enabled the functional analysis of fossil crania, offering a quantitative framework for evaluating hypotheses related to diet, tool use, and evolutionary changes in skull morphology (Smith et al., 2015; Gröning et al., 2011; Ledogar et al., 2016; Toro-Ibacache et al., 2016; Wroe et al., 2018).

As with any form of modelling, however, simplifications are required. This is particularly the case when working with fossil material, where the original soft tissues are no longer preserved. Several assumptions must therefore be made regarding how the model is constructed and loaded. These include the materials represented (Toro-Ibacache et al., 2016), the material properties assigned to bone and teeth (Herbst et al., 2021), and the muscle forces applied to the skull (Panagiotopoulou et al., 2017). For example, the physiological cross-sectional area (PCSA) of muscles, needed to estimate force magnitude, is unknown in fossil specimens, as are activation levels that determine muscle recruitment during feeding and biting tasks. Similarly, fossilised bone no longer retains its original properties, meaning that researchers must substitute plausible modern analogues for cortical and trabecular tissues (Ross et al., 2005). Sensitivity analyses have been used to test how these assumptions affect model outputs, and validation studies on living species have helped identify which parameters most strongly influence strain distribution (Panagiotopoulou et al., 2011; Godinho et al., 2017). However, almost all work in this area has focused on the muscles of mastication in relation to the crania or mandible.

A complementary source of information comes from electromyography (EMG), which records muscle activation patterns during specific behaviours. EMG can help researchers to understand variables such as timing and intensity of muscle activation for different feeding tasks and behaviours. Research on both humans and non-human primates has documented activation of the major jaw adductors (the temporalis, masseter, and medial pterygoid) during biting and chewing behaviours of varying intensity and direction, depending on the food being consumed (González et al., 2001; Fassicollo et al., 2021), its placement in the mouth and the gape required (Espinosa & Chen., 2012). Such data help to refine and validate finite element models by providing more physiologically realistic input forces.

While most paleoanthropological research has focused on the role of the masticatory muscles in craniofacial loading, electromyographic (EMG) studies have also recorded activity in several neck extensors during certain biting and clenching behaviours (Ciuffolo et al., 2005). These muscles include the sternocleidomastoid, trapezius, splenius capitis and semispinalis capitis, which act primarily to extend the head and stabilise the cranium against flexion. Much of the work investigating these muscles has been clinically oriented, focusing on their involvement in cervicogenic headache, temporomandibular joint disorder, and cervical spine mechanics (Giannakopoulos et al., 2013; Testa et al., 2015; Sagl et al., 2024). From this research, it appears that the neck muscles may become active during particular biting tasks, although which bites elicit the strongest activation has not been fully investigated, nor has this been considered in the context of human evolution.

Current finite element models of fossil hominins typically omit the neck musculature (Grine et al., 2010; Wroe et al., 2018), a simplification that has not been explicitly tested. It may be that activation of these muscles during straightforward vertical bites has only a negligible influence on craniofacial strain, and in such cases, their exclusion from existing vertical-bite simulations could be justified. However, the situation is likely more complex. Even modest anterior or asymmetrical loading of the dentition would tend to flex the head, requiring the neck extensors to contract to counteract that movement and stabilise the cranium.

What remains unknown is the magnitude of this activation during different biting tasks and how such counter-flexion forces influence craniofacial strain patterns. If these muscles generate even small opposing loads during vertical bites, they could alter local strain magnitudes and directions across the facial skeleton. Under more extreme anterior or asymmetric loading conditions, the stabilising forces produced by the neck extensors could be substantially higher, potentially modifying strain patterns throughout the craniofacial region. This is particularly relevant in the context of the anterior dental loading hypothesis, which proposes that some fossil hominins (most notably Neanderthals) regularly used their anterior teeth to grasp or pull objects, effectively employing the dentition as a third hand (Clement et al., 2012). Such behaviours would generate anterior or asymmetric loading of the skull rather than purely vertical compression, producing mechanical demands different from those involved in conventional biting or chewing. If these forces were substantial, they could have influenced craniofacial form and adaptation, making it essential to understand how the head and neck interact mechanically under these conditions.

These modelling uncertainties have two important implications. First, it is possible that current finite element models are under-loading the skull even during simple vertical bites by omitting counter-flexion forces that occur *in vivo*. Second, if anteriorly directed loads produce distinctly different strain distributions, then fossil-based interpretations of feeding behaviour and functional adaptation may be misleading, as they are derived from models that do not accurately replicate the mechanical environment. Therefore, addressing these questions is critical to improving the biomechanical validity of FEA studies and refining our understanding of how craniofacial structures respond to and evolve under complex loading regimes.

1.2 Thesis Rationale

Finite element analysis has been adopted by researchers from multiple disciplines as the go to method for biomechanical analysis of biting behaviours. However, the methodological protocol being used has substantial simplifications that may affect the reliability of the models being produced.

A major anatomical limitation in most published models could be the omission of neck musculature. Many models, particularly in areas such as palaeoanthropology, load only the muscles of mastication when testing biting scenarios, which may lead to an unrealistic and potentially unbalanced model of the skull. Testing this omission is vital as *in vivo* studies have documented increased activation of these muscles during biting, suggesting that their inclusion may be necessary for producing a realistic FE model.

A second limitation in the majority of FE models presented is that only static vertical biting scenarios are tested. While such loading conditions may be adequate for some research questions they unlikely capture the broader range of forces experienced during paramasticatory behaviours, where food, tools, or other materials may be clamped between the teeth and pulled with the hands. Excluding these behaviours can risk overlooking important aspects of how the skull experiences and dissipates load during everyday activities. Testing a wider range of loading scenarios would provide a more comprehensive understanding of craniofacial biomechanics, as different behaviours are likely to produce distinctive patterns of strain magnitude and distribution. Addressing this issue is therefore essential, since variation in loading direction and magnitude could alter previous conclusions about whether anterior dental loading contributed to adaptive bone responses in the craniofacial skeleton.

A third limitation affecting finite element models, particularly those of fossil hominins, is the way in which muscle forces are estimated and applied. In published FE models, muscle force is typically calculated as the product of the physiological cross-sectional area (PCSA), the intrinsic stress of the muscle, and the level of activation (O'Connor et al., 2005; Toro-Ibacache et al., 2016; Reddy et al., 2024). For living species, these parameters can be measured or estimated with some accuracy, but for fossilised specimens with no soft tissue, each component must be approximated. Muscle PCSA is often inferred from the dimensions of bony attachment sites or from scaled muscle reconstructions (Ross et al., 2005), while activation levels are assigned randomly or borrowed from unrelated taxa (O'Connor et al., 20005; Wroe et al., 2007). These simplifications mean that the relative activation between muscles, and therefore the distribution of applied forces, may not reflect true physiological patterns.

Previous sensitivity analyses have shown that even small changes in muscle activation or force magnitude can substantially alter craniofacial strain predictions (Bright & Rayfield., 2011; Fitton et al.,2012; Toro-Ibacache & O'Higgins., 2016). This uncertainty is heightened when considering that neck musculature and the corresponding activation data are almost entirely absent. To evaluate how much these assumptions affect model reliability, this study records *in vivo* surface EMG data from both the masticatory and neck muscles during controlled biting and pulling tasks. This data is then used to generate FE models loaded with real activation patterns, allowing direct comparison with previous simplified, estimated-force models. The results provide a base for assessing how activation assumptions influence strain outcomes and whether simplified inputs can still provide valid conclusions, an essential question for fossil focused research, where direct muscle data is unobtainable.

Overall, this study looks to improve the reliability of hominin skull models by addressing common gaps in published methodologies. More realistic loading may help to improve the reliability of models for anterior dental loading research for humans and potentially other hominin - although *in vivo* neck muscle data may be less appropriate for fossil hominin models.

The subsequent sections of this thesis are guided by the following questions:

a) To what extent does the inclusion of neck musculature influence craniofacial strain predictions during anterior biting, and should it be considered a necessary addition to finite element models?

b) How does changing the direction and nature of anterior loading (vertical versus pulling) affect predicted craniofacial strain patterns?

c) How do models loaded with *in vivo* muscle activation data compare with those using forces estimated from cadavers in terms of predicted strain magnitudes and distributions?

1.3 Thesis Aims

The aim of this thesis is to investigate the role that the neck musculature plays in influencing craniofacial strain during biting behaviours. In particular, it examines how paramasticatory loading behaviours, such as anterior pulls on the anterior dentition, are likely to engage the neck musculature and thus may alter craniofacial strain patterns. By integrating *in vivo* surface electromyography (sEMG) data with finite element (FE) modelling, this research assesses how the inclusion of neck muscles and more realistic loading scenarios influence model outcomes and interpretation.

The objectives for this thesis are to:

1. Develop a finite element model capable of simulating masticatory and paramasticatory loading, with the inclusion of neck musculature.

2. Evaluate whether the inclusion of neck musculature alters craniofacial strain patterns during anterior and vertical biting.

3. Record *in vivo* surface EMG data from the masticatory and neck muscles during different biting and pulling tasks to establish realistic muscle activation patterns.

4. Apply these activation patterns to the FE model to test how more realistic loading conditions influence predicted craniofacial strain distributions.

1.4 Thesis Structure

Chapter 2 will break down and discuss the topic of craniofacial biomechanics and the methods used for analysis in more detail. With a focus on reviewing published literature this chapter will aim to create a contextual understanding of the methodologies and findings presented in this thesis.

Chapter 3 (journal style) examines finite element analysis (FEA) in greater depth to provide a comprehensive overview of the method and its application within this study. Sensitivity testing will be conducted on a human female model to evaluate how input parameters and boundary conditions influence craniofacial strain patterns, while ensuring consistency with established protocols in craniofacial biomechanics. Once the standard model has been created, neck extensor muscles will be incorporated to assess their biomechanical influence. This will allow for the evaluation of how neck musculature affects strain distribution, offering insights into the importance of including these anatomical structures in human craniofacial models.

Chapter 4 (journal style) introduces surface electromyography (sEMG) and its application in validating finite element models. Unlike the theoretical force estimations used in Chapter 2, this chapter collects and incorporates empirical data obtained from a live human subject performing paramasticatory behaviours. By measuring the actual forces generated during anterior pulling (e.g., pulling on a leather belt with the teeth) and recording muscle activation in both the masticatory and neck extensor muscles during these tasks and during maximum vertical biting, more physiologically realistic loading conditions were established. This data is then used to refine the finite element models developed in Chapter 3, allowing for more accurate simulation of real-world biting and pulling behaviours. This approach bridges the gap between theoretical modelling and *in vivo* biomechanics, offering a more robust test of how the human craniofacial skeleton responds to paramasticatory loading.

Chapter 5 discusses the results collected in the previous chapters in a literary context and explore possible directions for future craniofacial biomechanics-based research. This will conclude with an optimistic look at where the discipline may be headed, and how it might get there.

Finally, Chapter 6 will conclude the thesis by revisiting the aims set out in chapter 1 and discuss the outcomes of the research and its applicability to various disciplines.

Chapter 2: Loading the Skull

2.1 Craniofacial Skeleton

The human skull is the most complex portion of the skeleton, composed of twenty-two bones. It is divided into the neurocranium (brain case) and the viscerocranium (facial region). Together they protect the brain along with the sensory organs; the tongue, olfactory receptors, eyes, and ears (Becker, 2023). In order to safely encase the brain, the bones of neurocranium are joined together via sutures, at birth these sutures are open and slowly fuse together during childhood, these are a type of fibrous synarthrodial joint that do not allow any movement.

The primary function of the skull is to protect the brain, eyes, and inner ears. As the brain is an extremely delicate and vital organ, it is important that the skull can withstand the forces imposed upon it during daily activities (Anderson et al., 2023). Another function of the skull is to provide structure for the face: supporting the muscles, blood vessels, and nerves that allow for movement in the face for various communication, respiration, and mastication actions (Kuschmider, 2024). The forces enacted upon the skull during essential use are known as loads, and the actions that cause these forces are known as loading behaviours.

2.2 Masticatory Loading

One of the most taxing loading behaviours that the skull encounters multiple times each day is mastication. Mastication is a complex process that uses rhythmic mandibular movement to manipulate food: crushing between the teeth in preparation for swallowing and digestion (van de Bilt et al., 2006). These mandibular movements are facilitated by the muscles of mastication; masseter, temporalis, and the medial and lateral pterygoids (Basit et al., 2022).

2.2.1 Muscles of Mastication

The temporalis muscle is fan shaped and originates across the temporal line from the temporal fossa to the inferior temporal line, with three layers of fibres each with their own orientation: anterior fibres orientated vertically; mid fibres orientated obliquely; and posterior fibres orientated more horizontally (Basit et al., 2022). All of the temporalis fibres pass between the skull and the zygoma, to attach on the coronoid process of the mandible by two distinct tendons, as shown in figure 1.01 (Yu et al., 2021). As well as the muscle, the temporal fascia is thought to contribute to the biomechanics of the masticatory system by reducing strains in the zygomatic arch due to its thin and superficial, and deeper, more fibrous layers (Curtis et al., 2011). Generally speaking, the temporalis muscle has the largest cross-sectional area (CSA) and is therefore one of the strongest muscles of mastication (Maughan et al., 1983; van Spronsen., 2010). The main functions of the temporalis muscle are the elevation and retraction of the mandible which are done by the anterior and posterior fibres respectively (Gaillard et al., 2009).

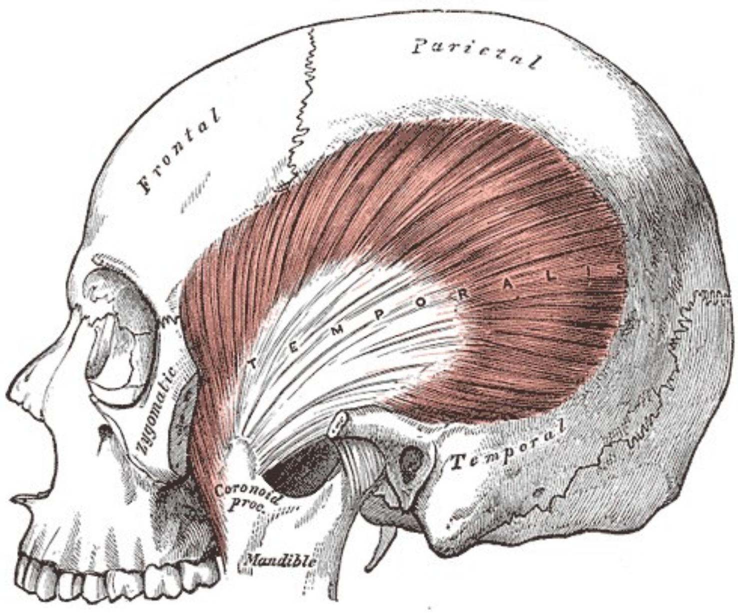

Fig 2.01: Illustration of the temporalis muscle and its attachment sites.
(Henry Gray 1918, as cited by Henry Vandyke Carter 2007).

The masseter is a multipennate muscle that is quadrilateral in shape and originates on the infero-anterior portion of the zygomatic arch, with three layers of fibres all with similar orientations and inserting along the mandibular ramus (Corcoran & Goldman, 2022). The superficial masseter fibres are longer than those of the deeper portions, with the intermediate and deep layers being described as more fan-shaped (Toro-Ibacache, 2013). Despite being made up of three portions, the masseter is often described as just two parts when interpreting function due to the split in work appearing in the anterior and posterior regions (Basit et al., 2022; Corcoran & Goldman, 2022). Fibre composition of the masseter is seen to vary across individuals which is suggested to relate to varying levels of utilisation and adaptability to hyperactivity (Ibebunjo et al., 1996). Based on muscle force output per kilogram, the masseter is the strongest muscle in the human body and so is critical to the bite force achieved by the masticatory system (Library of Congress, 2019). The main function of the masseter is the elevation of the mandible; however, it can also aid in the protrusion of the jaw (Vasković, 2022).

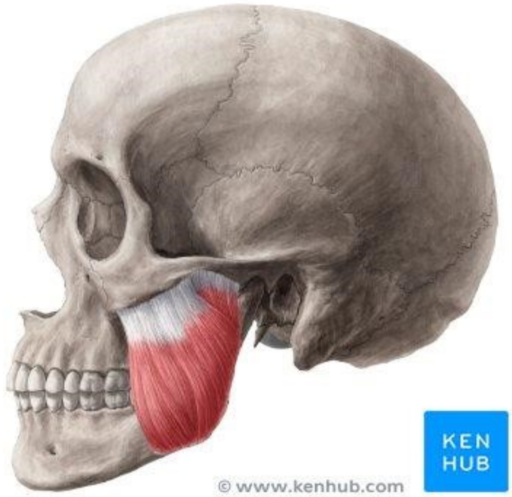

Fig 2.02: Illustration of the masseter muscle and its attachment sites.
(Vasković, 2023).

Both the medial and lateral muscles are split in two at their insertion but they then converge to a single attachment. The medial pterygoid is rectangular in shape with the superficial head originating at the maxillary tuberosity of the inferior maxilla, and the deep head originating from the medial surface of the lateral pterygoid plate of the sphenoid bone (Basit et al., 2022). The upper head of the lateral pterygoid is more triangular in shape and originates at the inferior temporal surface of the greater wing of the sphenoid bone whilst the lower head originates from the lateral aspect of the lateral pterygoid platen of the sphenoid bone (Basit et al., 2022). The medial pterygoid inserts at the medial ramus of the mandible whilst the lateral pterygoid inserts on the pterygoid fovea of the neck of condylar process (Jain & Rathee, 2022). The medial pterygoid is the most pennated of the four primary muscles of mastication, with multiple tendinous sheets separating the muscle in its upper third (Toro-Ibacache, 2013). The main function of the lateral pterygoid is mandibular depression, it is the only muscle of mastication that does so (Lehr & Owens, 1980). On the other hand, the medial pterygoid exerts approximately 1.6 times the force of the lateral pterygoid whilst performing its functions of mandibular protrusion, lateral movement, and elevation (van Eijden et al., 1995).

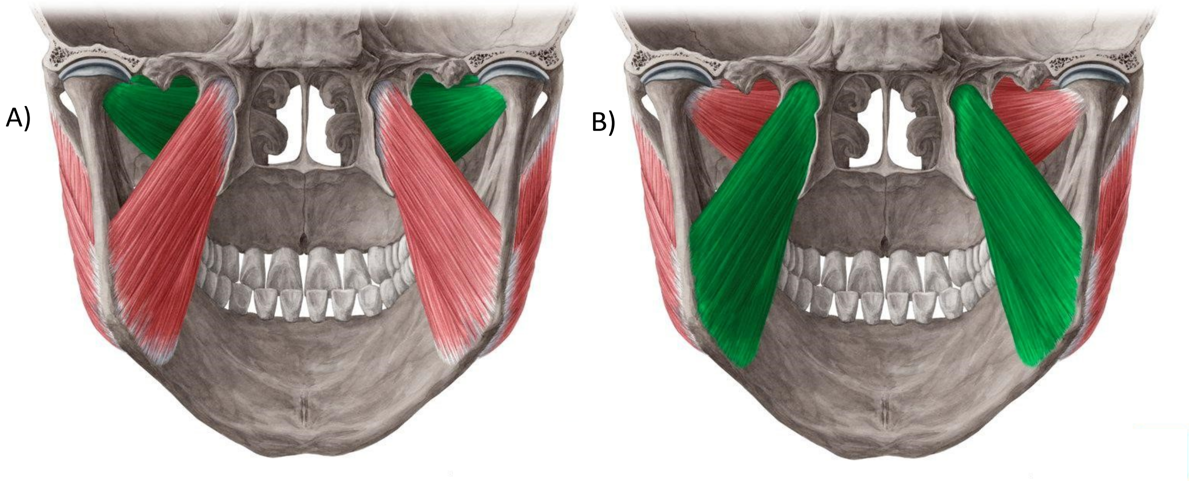

Fig 2.03: Illustration of the a) lateral and b) medial pterygoid muscles and their attachment sites. (Grujičić, 2023).

All of the masticatory muscles work together to support mandibular movement in all three planes of motion in order to chew/grind food (Basit et al., 2022). Due to the multipennation of the muscles of mastication there is an increased number of muscles fibres within a limited space thus increasing the intrinsic muscle strength, which is necessary for efficient chewing movement (Hannam & McMillan, 1994). As the muscles of mastication contract together they generate force which acts upon the skull to enable the movement of the mandible. This movement is created by electrical signals which can be measured using techniques such as electromyography which uses these measurements to analyse the activation levels of each muscle. Such methods have detected that masticatory muscle activation during repeated chewing motions are subject to variability with each movement (Ivanenko et al., 2004).

2.2.2 Bones, Teeth and the Temporomandibular Joint

The skeletal element of the masticatory system is essential for withstanding the forces applied to the area during a bite as they absorb the mechanical stress and allow for proper function of the whole system (Currey, 1962). The skeletal components of mastication also provide the support system that allows movements such as chewing to take place, these components are; the maxilla, the mandible, and the temporal bone which allows the mandible to articulate to the skull via the temporomandibular joint (TMJ) (Zezo, 2015). The TMJ is a hinge joint that allows the jaw to act as a lever during biting behaviours, this type of joint is stable and allows force to be distributed evenly over a wide surface (Oliver, 2010; Luo, 2019).

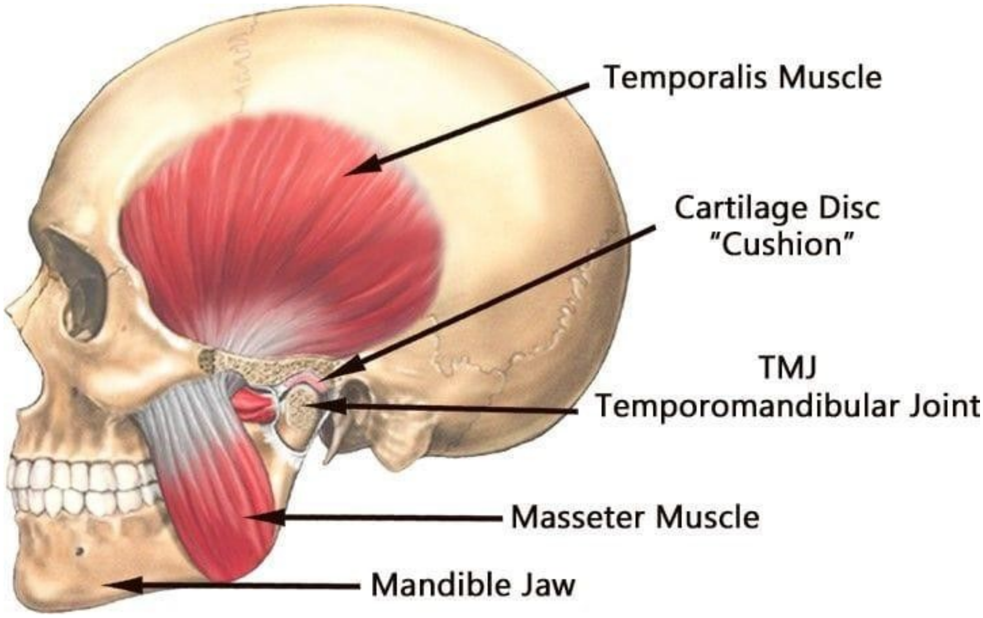

Fig 2.04: Illustration of the temporomandibular joint with relevant anatomical features highlighted. (Equilibrium Physiotherapy, 2019).

The TMJ is one of the most complex joints in the human body and is key to facilitating the movements needed for normal function of the jaw during masticatory loads (Herring & Liu, 2001). Due to its complex nature and the repeated and heavy forces it endures, temporomandibular disorders (TMD) are fairly common due to the mechanical stresses that are implemented upon it during a lifetime (Sagl et al., 2024). These same forces that cause mechanical stresses are also thought to be responsible for shaping the craniofacial skeleton and are considered a major factor for the variation seen across human populations throughout history (Paschetta et al., 2010; Brachetta-Aporta & Toro-Ibacache, 2021).

During mastication or biting activities, the mandible first depresses to open the mouth, a movement assisted by gravity and the activity of jaw-opening muscles such as the digastric and lateral pterygoid (Rathee & Jain., 2022). To close, it is then elevated by contraction of the major jaw adductors (masseter, temporalis, and medial pterygoid) which raise the mandible and bring the mandibular and maxillary teeth into occlusion. The magnitude and direction of these muscle forces vary with the position and properties of the item between the teeth (Panagiotopoulou et al., 2023), influencing how loads are transmitted through the dentition and craniofacial skeleton.

The teeth themselves play distinct functional roles: incisors are suited to food acquisition and incision due to their bladed shape; canines can assist in piercing; premolars and molars facilitate grinding and crushing with broader occlusal surfaces, (PW. Lucas., 2004). Variation in tooth form and wear patterns among humans and other primates have frequently been studied in relation to different dietary or behavioural demands (Molnar et al., 1972; Le Cabec et al., 2013), and these differences likely influence the distribution of forces within the masticatory system and skull (Ross et al., 2005; Panagiotopoulou et al., 2011; Fitton et al., 2012). The mechanical strains generated during occlusion are dissipated through the mandible, the temporomandibular joint, the craniofacial skeleton, and the cranial vault, meaning that craniofacial morphology and muscle arrangement together will determine how the skull resists these loads.

2.2.3 The Role of Neck Muscles During Masticatory Loading

Whilst masticatory muscles and the jaw are the primary components of masticatory loading, neck muscles can also play a key role in these actions. When masticating, muscles at the back of the head and neck co-contract with the masticatory muscles in order to stabilise the head and neck during the exertion of varied forces (Moon et al., 2015). Neck extensor muscles are the main group responsible for the stabilisation of the head and for segmental movement of the cervical spine (Schomacher & Falla, 2013).

The sternocleidomastoid is a large anteriorly positioned superficial muscle that originates on the upper medial quarter of the clavicle and the top of the manubrium and inserts on the mastoid process of the temporal bone (Sendić, 2022). It is also rich in anaerobic fibres and so is useful for quick strong movements, becoming less so over long periods of contraction (Meznaric et al., 2017). Because it is such a large muscle within the neck, it has multiple functions, including the rotation of the head, inclination, and extension of the neck, and it is also known to assist with inspiratory movement (Bordoni & Varacallo, 2022). During masticatory loading it is known that SCM activity increases with larger boluses of food and harder textures, this change in activity links it intrinsically with jaw function (Häggman-Henrikson et al., 2013).

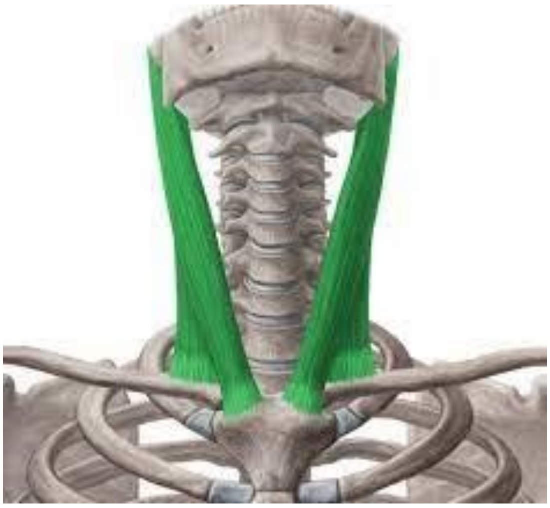

Fig 2.05: Image of an isolated sternocleidomastoid muscle (Karunaharamoorthy, 2022).

The trapezius is a large triangular shaped superficial muscle that when viewed with its counterpart looks like a trapezoid shape (Sendić, 2022). Whilst technically a back muscle, it is split into three portions which also functionally assist with the neck. The superior fibres originate on the medial third of the superior nuchal line, the external occipital protuberance, and the nuchal ligament and inserts onto the distal third of the clavicle (Bakkum & Cramer, 2014). The middle fibres of the trapezius originate on the spinous processes and supraspinous ligaments of vertebrae T1-T4 and insert at the medial acromial margin and superior crest on the spine of the scapula (Knapp, 2021). The inferior fibres originate on the spinous processes and supraspinous ligaments of vertebrae T4-T12 and insert at the lateral apex of the medial end of the scapula spine (Sendić, 2022). Because it is such a large muscle spanning across the upper to mid back as well as the neck, it has several functions - the most relevant being the superior fibres which work to extend the neck and elevate and rotate the scapula (Ourieff et al, 2022). The upper portion of the trapezius, also known as "trapezius pars descendens" is commonly cited in electromyography papers that study jaw related behaviours such as clenching as it is known to be affected by TMD (Lodetti et al., 2012; Giannakopoulos et al., 2013).

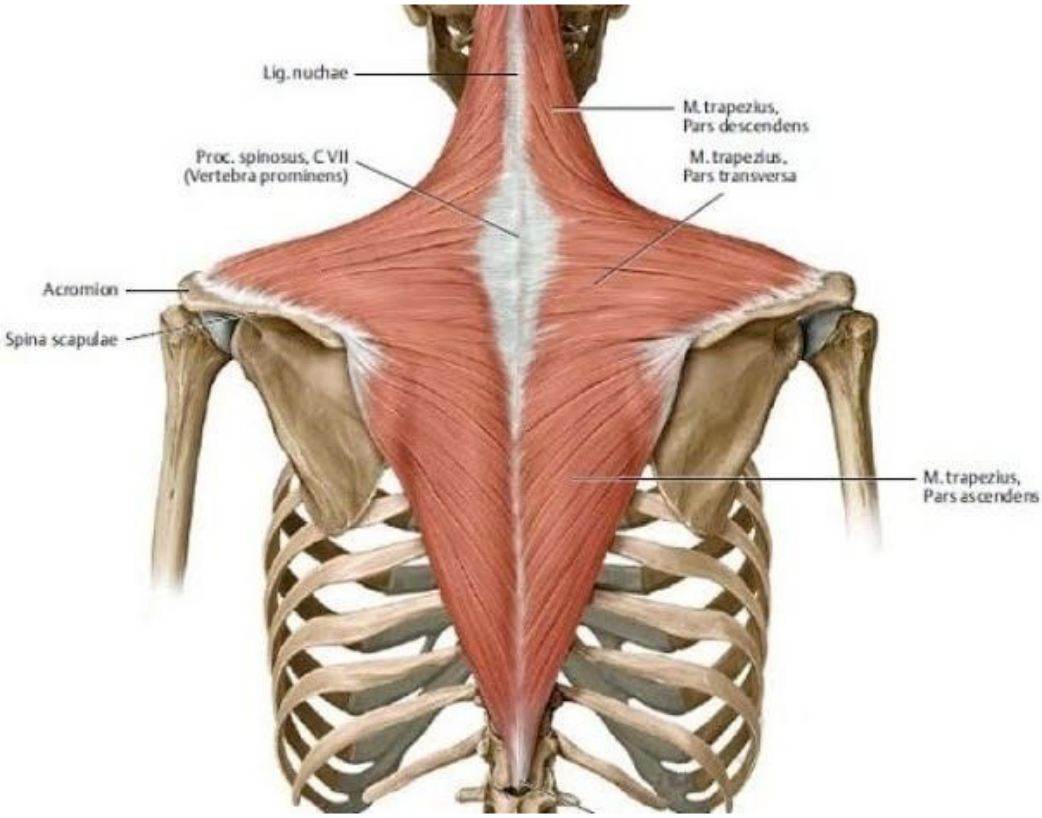

Fig 2.06: Illustration of trapezius with labelled portions descendens, transversa, and ascendens (MSK Neurology, 2019).

Deep to the trapezius muscle lies the splenius capitis and cervicis muscles. The splenius capitis is a paired muscle that sits on top of the semispinalis capitis and originates on the spinous processes of vertebrae C7-T3, as well as the nuchal ligament and attaches at the lateral superior nuchal line of the occipital bone and the mastoid process of the temporal bone (Shahid, 2016). When acting bilaterally the splenius capitis functions to extend the neck and cervical spine, and when acting unilaterally flexes and rotates the neck laterally (Winer, 2020). Like the splenius capitis, the splenius cervicis extends the neck when contracted bilaterally, and flexes and rotates the neck laterally during unilateral contraction (Sendić, 2022). While the splenius capitis does not directly interfere with the masticatory process itself, it is known to tighten the jaw when it is opened wide, thus placing itself in one of the "most complex inter-relationships of muscle groups in the human body" (Ernest & Ernest, 2011).

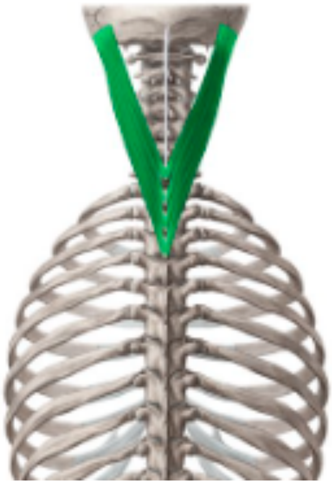

Fig 2.07: Illustration of an isolated splenius capitis muscle.
(Shahid, 2016).

Deep to the splenius capitis, lies another pair of muscles known as semispinalis capitis and semispinalis cervicis. The semispinalis capitis is the largest semispinalis muscle, originating at the articular processes of vertebrae C4-C7 and the transverse processes of vertebrae T1-T6 (Grujičić, 2022). The semispinalis capitis then inserts into the occiput below the superior nuchal line (Shimizu & Suzuki, 2010). The function of the semispinalis capitis, like the splenius muscles, is to extend the neck during bilateral contraction and flexes and rotates the neck laterally during unilateral contraction (Sendić, 2022). Like the splenius capitis it does not participate in masticatory behaviours itself, however it is known to co-contract during teeth grinding and clenching due to research on neck pains related to sleep conditions such as bruxism (Giannakopoulos et al., 2018).

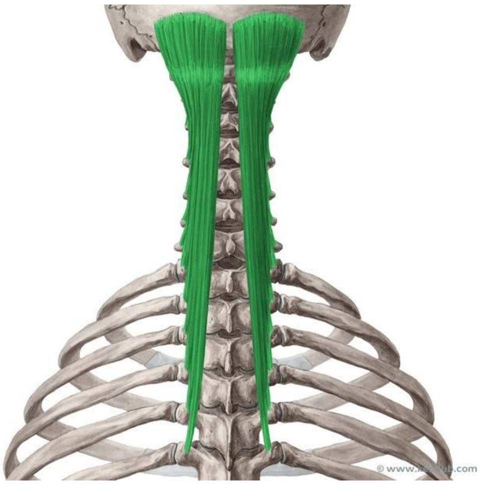

Fig 2.08: Illustration of an isolated semispinalis capitis (Grujičić, 2022).

Like the muscles of mastication, neck extensors such as the semispinalis capitis exert a force on the skull during masticatory loading as they contract downward during mouth opening (Moon et al., 2015). As the primary role of these extensors is to manage head stabilisation, they are adept at dispersing forces from elsewhere on the skull, this has been particularly well studied in slightly more extreme scenarios such as concussion or whiplash from contact sports (Eckner et al., 2014; Streifer et al., 2019; Cooney et al., 2022).

2.3 Mechanostat Theory

Mechanostat theory, first put forward by Frost (1987), describes how bones adapt their mass and architecture in response to mechanical loading (Lerebours & Buenzli, 2016). Mechanical loading refers to the physical stress that a mechanical system such as the masticatory system, experiences during physical activity (Vaia, 2023). This loading causes bones to change their structure and become stronger in response to heavy or prolonged mechanical stresses; this phenomenon is known as Wolff's Law (Tsubota et al., 2009).

Bone adaptation occurs when osteocytes convert mechanical strain into biochemical signals, which then initiate the remodelling processes of bone formation or resorption (Nomura & Takano-Yamamoto, 2000). Bone formation is carried out by osteoblasts under a high magnitude of or prolonged force, for example tennis players will develop larger bones in their playing arm compared to their resting arm (Robling & Turner, 2009). Bone resorption is performed by osteoclasts when there is a lack of loading on the bone, also known as atrophy.

This can occur when a person is bed bound for long periods of time, and in extreme cases such as astronauts not being subjected to Earth's gravity in space (Lloyd, 2023).

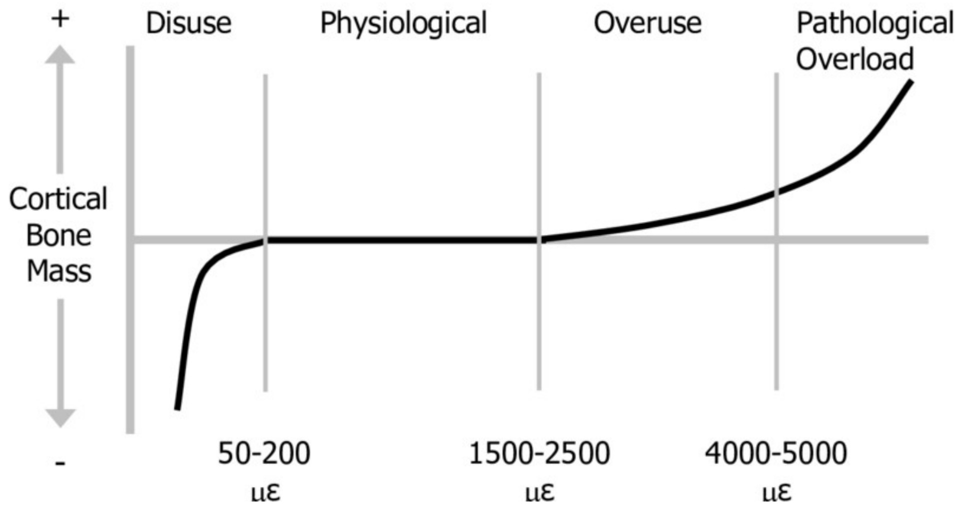

Fig 2.09: Graph depicting Frost's Mechanostat theory (Nagaraja, 2006).

The amount of strain placed upon the skull during loading determines the degree of the reaction of the bone to said force, this reaction can be classified into four categories: disuse window; adapted window; mild overload window; and pathologic overload window (Mahnama et al., 2013). The disuse window describes the scenario where bone experiences little to no strain and begins the process of resorption (Elsayed, 2019). The adapted window is considered the optimal level of strain for bone as it reaches equilibrium of modelling and remodelling, this usually occurs during normal daily activities (Khan et al., 2022). The mild overload window occurs when a higher level of strain is experienced and fatigue microfractures occur, which can be beneficial in the short term but lead to injury in the long term if not handled properly (Elsayed, 2019). Finally, the pathologic overload window presents extremely high levels of strain that cause fractures or formation of fibrous tissue, such as traumatic injuries or high-impact sports (Hedge et al., 2022).

While high magnitudes of strains are most commonly associated with bone remodelling, it can also be caused by low magnitude, high frequency loading (Dittmer & Firth, 2017). Due to repetitive loading behaviours such as biting, craniofacial bone adaptation begins during childhood but can continue during adulthood due to dietary changes or non-masticatory behaviours (Liang et al, 2024). Because of the repetitive nature of feeding, difference in diet has led to small variations in morphologies across human populations, with groups slowly adapting to the diets available in their environment (Menegaz et al., 2010).

2.4 Diet Variability and Skull Loading

Diet plays a significant role in loading and shaping the morphology of the skull. Long-term diets can shape the skull during childhood, both through the medium of mechanical stress, but also because of the nutrients that are absorbed or from malnutrition. The skull is the most sensitive part of the body to malnutrition, particularly in the early stages of life a lack of protein can lead to shorter and wider viscerocranium (Miller & German, 1999). So, it is known that changes in nutrient can affect the skull, but so can other variables of diet such as the size of the food and its consistency.

While nutritional content can influence skeletal development, the mechanical properties of food , such as its size, hardness, and toughness, also play a significant role. It has long been observed that general masticatory form is closely associated with habitual loading regimes, where individuals regularly consuming harder or more resistant foods tend to exhibit more robust craniofacial features (Menegaz et al., 2010). These mechanical demands, imposed by chewing and food processing behaviours, generate strains that may influence the development and maintenance of cranial structure through biomechanical adaptation (Stansfield et al., 2018).

The size and mechanical demands of food items in the human diet can vary considerably. For example, small items like pomegranate or pumpkin seeds require only minimal jaw movement and can be processed with a nearly closed mouth, whereas larger items such as apples often necessitate wide jaw gapes during biting. These differences influence not only the degree of temporomandibular joint (TMJ) movement but also the mechanical loading experienced by the skull (Ross & Iriarte-Diaz, 2014; Panagiotopoulou et al., 2023). Some studies have shown that small gapes can generate higher stresses in craniofacial structures compared to larger ones (Bourke et al., 2008), likely due to changes in jaw lever mechanics. At small gapes, the masticatory muscles operate with shorter moment arms, requiring greater muscle force to achieve equivalent bite forces (Laird et al., 2020). At very wide gapes, the orientation of the jaw muscles shifts, often resulting in a reduction in maximum bite force due to suboptimal mechanical advantage (Curtis et al., 2008). These biomechanical trade-offs indicate that food size and gape angle together can influence cranial strain and bite performance.

Fig 2.10: Man eating an apple, exhibiting a large gape (Christensen, 2009), and woman eating pomegranate seed, which will require only a small gape (Yakobchuk, nd).

As well as size, the consistency of food can have an effect on the mechanical strains created during masticatory loading. The human diet in the context of all animal diets is fairly soft due to the invention of cooking, with the raw meat and bones diet of animals like lions being considered as one of the hardest (Bastos et al., 2021). The variation seen in the human diet is vast, common food items like hard and brittle nuts, tough and chewy jerky, through to soft and silky tofu, all of which have different effects on craniofacial strains. The changes in strains caused by differences in food consistency are due to the varied mechanical properties of food. Hard and brittle food like nuts require a higher bite force but will fracture with little deformation and require less repeated movements, whereas tough and chewy foods such as jerky require many more repeated movements before they can be broken down for digestion (Schab et al., 2022). This difference in high versus repeated strain can have an effect on the muscles of mastication, as high forces can lead to an increase in size in order to increase strength, whereas repeated low forces can lead to microtrauma in the skull which is a precursor to bone remodelling (Hammond et al., 2019). As well as the possibility of bone formation due to harder items in the diet, a soft diet has also been known lead to bone resorption, particularly in the mandible (Fujita & Maki, 2018).

These theories behind morphological adaptations to mechanical loading of the masticatory system are corroborated by anthropological evidence in human history. Around 10,000 years ago there was an abrupt shift in the human diet as farming became a common practise, reducing the reliance in wild plants and hunting animals. This change made expanding to and sustaining large populations a possibility that would not have existed with the continued practise of hunter-gathering (von Cramon-Taubadel., 2017). This switch to an agricultural diet meant that the overall mechanical stress of the human diet was reduced, with even some of the earliest known farmers displaying more gracile skulls than foragers (Carlson & van Gerven, 1977).

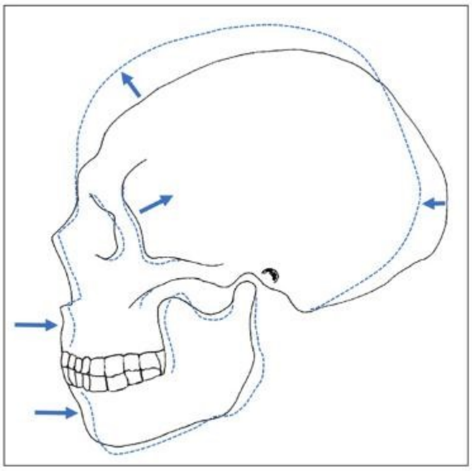

Fig 2.11: Summary of morphological changes observed in Nubian skulls through time from before (solid line) and after the introduction of farming (dashed line). (von Cramon-Taubadel, 2017).

More recently, increasing rates of congenital agenesis of the third molar have been reported, demonstrating a failure of the tooth structure to form during postnatal development (Scheiwiller et al., 2020). This congenital absence of the “wisdom tooth” has been linked to the gradual softening of the human diet and the gradual decrease in the size of the mandible and the maxilla (Gkantidis et al., 2021). These findings demonstrate the significant effect that masticatory loading can have on the skull, and research by Baab et al (2010) confirms that variation in the robusticity of modern human skulls are more closely linked to masticatory loading than climate or genetic distances.

Overall, it can be seen through anatomical research of both past and present humans, that the skull is sensitive to the loads placed on it via the masticatory system. However, masticatory loading due to feeding is not the only source of mechanical strain on the masticatory system in daily life. Humans are also seen to commonly use their teeth as tools on a daily basis; this is a behaviour known as paramasticatory loading.

2.5 Paramasticatory Loading

Paramasticatory behaviours are defined as actions that require the loading of the masticatory system, without the ingesting of food, for example using teeth to open a packet, or holding a material between the teeth while crafting (Willman, 2016). Both of these load types are thought to produce similar forces on the skull, however there is a lot of debate surrounding the impact of paramasticatory behaviours on morphological adaptations, as it is generally thought that the paramasticatory behaviours do not play as big a role as food processing (Wang et al., 2010).

Generally speaking, in modern western society there is little need for the use of paramasticatory loading to reach the requirements for skeletal adaptation due to the preprocessing of foods and abundance of tools catered to all aspects of daily life. Despite all of the tools available, it is still instinctual for people to use their teeth for a vast array of paramasticatory behaviours such as; tearing open packets, biting nails, chewing pen lids, carrying items when their hands are full or busy, or tightening knots, to name a few. Another common behaviour that is done without thinking would be bruxism (grinding of teeth), this is often done unconsciously and the high force and frequency can have a severe effect on dentition and the masticatory and neck muscles (Giannakopoulos t al., 2013).

Paramasticatory activities are also observed in specific cultural groups through the use of ethnography. Primarily using field studies, researchers have managed to record how specific groups use their teeth for cultural practices, social hierarchies, and resource manipulation (Edinborough & Radovic, 2015). Most often ethnographic studies are used to give meaning to behaviours that have been associated with fossil hominin and confirm theories derived from the archaeological record (Krueger & Ungar, 2010).

Inuit communities have been subject to a great deal of research for many years, as a hunter-gatherer population that existed for around 10,000 years before western influence, they still followed a traditional lifestyle that has been a valuable source of comparison for many anatomists and archaeologists (Spencer & Demes, 1993; Ungar et al., 1997; Stewart, Keith & Scottie, 2004; Betts, 2007; Wang et al., 2010; Clement et al., 2012; Krueger et al., 2012; Fiorenza et al., 2013; Friesen, 2013; Le Cabec et al., 2013). Traditional Inuit camps have a division of labour with a strong gender component, although it is not absolute. Generally, the men in the group go hunting and fishing, while the women take care of the children, clean, prepare clothes, process food, and cook (New World Encyclopaedia, 2008). Due to this division in labour, there is also a different tool kit for men and women, with women using tools such as Ulu's which they used for meat and hide preparation, and men using tools such as snow knives, snow probes, and shovels (Kalluak, 1999). This split in daily tasks sees different levels of dental wear for males and females within the same population. Two studies of the same sample, which were performed 33 years apart from the Igloolik island community found that males were shown to have higher levels of molar wear attributed primarily to bruxism, however, their female counterparts are shown to have much higher amounts of anterior dental wear (Tomenchuk & Mayhall, 1979; Clement & Hillson, 2012).

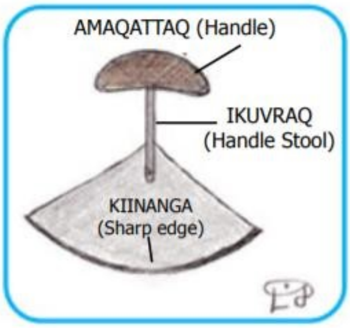

Fig 2.12: Variation of an Ulu used by Inuk women to cut meat (Kalluak 1999, p. 1, fig 1).

Being a nomadic group that uses complex stone tools and dress in clothes made of animal hide, they are the topic in many studies looking to draw comparisons for Neanderthal paramasticatory behaviour, particularly because they are known to use their teeth-as-tools for a variety of tasks, such as processing animal hide using their anterior dentition (Krueger, 2011). Specifically, Inuit in Greenland are known to soften seal hide with their teeth, which creates significant dental wear on their anterior teeth (incisor and canine) in comparison to their molars (Clement et al., 2012). This outcome is often what links them as a primary point of reference to Neanderthals, who also had significantly more wear on their anterior dentition. However, the comparison of their morphology and behaviours does not stop there, Inuk people have been found to have more favourably positioned masticatory muscle mandibular attachments for heavy or repeated loads than the average extant non-hunter-gatherer, likely due to their consistent use of heavy paramasticatory loading in comparison to less traditional populations (Spencer & Demes, 1993).

Fig 2.13: Inuk woman softening seal hide with her teeth (Dobbin, 2017, fig 4).

Another group that is often cited in relation to paramasticatory behaviours, is the Cherokee Nation. The Cherokee Nation are a large community that has settled in most of the South-eastern states in the USA for more than 3,000 years. The Cherokee communities are known to live off the land by cultivating and growing their own crops and keeping chickens, as well as traditionally hunting wild game such as deer and bison (Chiltoskey, 1976). Like the Inuit, there is a division of labour whereby the men in the community hunt using a variety of tools. Depending on the game that they were hunting they included blowguns, flint knives and bow and arrows. The women in the community would stay at the camp, tending to the crops and the home (Blakely and Beck, 1984). Since traditional Cherokee did not use their teeth to hold hide during scraping activities, it has been speculated that their considerable anterior dental wear instead came from pulling plant fibres between their teeth in the process of manufacturing cordage, basketry, sinew, or cloth. This behaviour has been documented amongst historic Native American fishing groups in the vicinity of Stone Lake, California, with the use of teeth during basketry, line, and net manufacturing (Schulz, 1977). This difference in use can be seen in dental microwear in a study by Schulz (1977) where striations on the occlusal surface could be seen with a consistent width, travelling in the linguo-labial direction.

A study by Spencer and Ungar (2000) compared the craniofacial form of specimens from three historical Native American populations that are known to have used varied subsistence strategies. They discovered multiple differences in their craniofacial morphologies that they attributed to incisor loading using ethnographic data and incisal microwear data from their parallel study (Ungar & Spencer, 1999). It was found that the Aleut specimens, who lived in a culture of high force/frequency paramasticatory loading, had the most well adapted masticatory muscle positioning and mandibular robusticity.

The Hadza tribe of Tanzania has also been observed to use their teeth as tools, particularly when making hunting instruments like arrows (McCabe, 2017). The women in the tribe are also known to peel tubers and manipulate leather with their teeth (Berbesque et al., 2012). In conjunction with these behaviours the Hadza tribe is seen to have morphological traits commonly associated with paramasticatory loading such as mild midfacial prognathism (Ikeda & Hayama, 1982). As highlighted in the passages above there are multiple sources of evidence that demonstrate a relationship between paramasticatory loading and adaptive cranial morphology in humans.

The concept of paramasticatory loading can be seen not only in human populations, but also in primates. One example of this would be marmosets and their use of anterior dentition to gouge tree bark in order to reach the sap inside for consumption (Hogg et al., 2011). Whilst tearing tree bark with the incisors is not unique to the marmosets, removing it in this manner without consuming the bark is (Thompson et al., 2014). This activity requires a high magnitude of force on their masticatory system, and taking up around 70% of their day it is also a very highly repeated behaviour, so it is expected that there would be some sort of impact on their craniofacial morphology (Vinyard et al., 2009). In a 2009 study by Vinyard et al, it was found that these tree gouging marmosets had better adapted masticatory muscles and TMJ positioning than marmoset populations that did not habitually perform tree gouging. This again demonstrates that the forces enacted on the skull while performing paramasticatory loads can likely be high or frequent enough to cause plastic adaptation during an individual’s lifetime.

Fig 2.14: Marmoset performing tree
gouging action in a laboratory setting
(Eng et al, 2009)

Tai chimpanzees have been known to modify tools made from sticks with their teeth, in order to achieve their desired length and sharpen the ends (Boesch & Boesch, 1990). Chimpanzees have also been seen to make spears up to 63 centimetres long to hunt smaller mammals, again sharpening them with their teeth (Hooper, 2007). Following that their use of teeth as tools is a habitual part of their diet acquisition strategy, it is no surprise to see that regions of the skull such as the zygomatic arch and the brow ridges are much better suited to withstanding these sorts of loads than the average modern human skull (Himme, 2013). however, it is worth remembering that these differences will not be entirely related to paramasticatory loading as chimpanzees are known to have a significant hard and tough aspect to their diet, which will also contribute to the overall robustness of their skulls (Taylor et al., 2008).

Fig 2.15: Chimpanzee biting a large stick for shaping into a tool
(Price, 2010).

Many of these differences in skull morphologies have the potential to be caused by multiple environmental variables. One way in which researchers try to discern which features may be a product of loading of the skull versus genetic or other environmental factors, is the method of Finite Element Analysis.

2.6 Finite Element Analysis

Finite Element Analysis is a technique that uses computer simulations to predict mechanical reactions to parameters such as stress, heat, or fluid flow (Autodesk, 2022). In an anthropological context it is most often used to predict a skeletal model's biomechanical reaction to the forces of specific loading scenarios. When performing finite element analysis (FEA), it is critical that certain boundary conditions are followed in order to successfully test these virtual biomechanical models, boundary conditions include; forces that are balanced in order to prevent the model spinning indefinitely, materials such as bones or teeth must be given physical quantities so that the program can predict their reaction to the forces applied, and strain-displacement relations that are used to measure the deformation undergone by the model due to the external forces (Brush, 2019). Results are then interpreted as values of stress (σ) and strain (ε). These stresses and strains are displayed as colourful patterns on the model which are used to show the researcher where the model is experiencing high/low levels of stress or strain during certain scenarios.

A recent study by Kim et al (2024) demonstrates the application of finite element modelling to simulate occlusal loading in the human skull. The researchers created a high-resolution model of the cranium and mandible using anatomically accurate geometrics and assigned cortical and cancellous bone properties based on Misch's classification. Occlusal forces were distributed across the molars, while muscle forces were positioned to reflect anatomical origin and insertion points. Boundary conditions were implemented to constrain joint motion, ensuring mechanical stability throughout the simulation. The model was validated against clinical bite force data, allowing for accurate mapping of stress and strain across craniofacial structures. This approach highlights the importance of realistic force application and constraint modelling in evaluating biomechanical responses to masticatory loading.

In relation to paramasticatory loading, finite element models of hominid skulls are loaded with the scenario of a unilateral or bilateral bite, most often a bilateral (balanced) incisor bite (Gröning et al., 2011; Shi et al., 2012; Ibacache, 2013; Commisso et al., 2015; Prado et al., 2016; Toro-Ibacache et al., 2016; Godinho et al., 2017). These modelling scenarios predict how the skull responds to feeding behaviours, including the associated muscle forces, bite reactions, and joint reaction forces applied at specific locations.

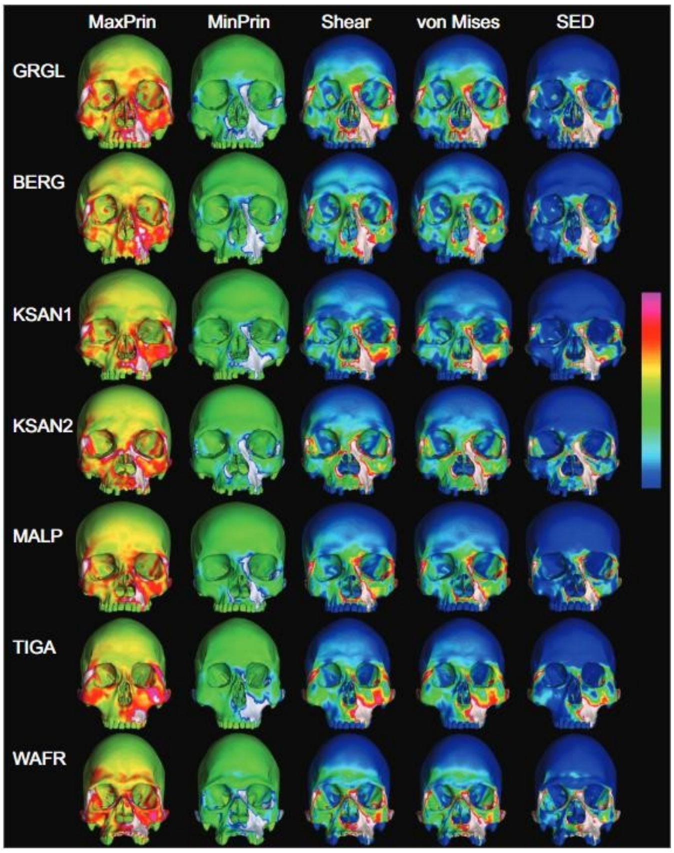

Fig 2.16: Comparative display of global strain maps from finite element testing of human specimens. (Ledogar et al, 2016, p. 22, fig. 7).

A study by Ledogar et al. (2016) used finite element analysis to test whether the modern human or *Pan troglodytes* craniofacial skeleton is better adapted to withstand high magnitude bite forces. To account for the variation within the species they modelled the crania of multiple humans from different geographic regions. Their results found that although the human models were efficient at producing bite force, they were likely not adapted for high magnitude biting – rather they interpreted their results to mean this efficiency was developed as a byproduct of another, unrelated function. This study was well received with a large number of papers on human evolution citing their work (Katz et al., 2017; Wroe et al., 2018; Lacruz et al., 2019; Edmonds & Glowacka, 2020; van Casteren et al., 2022).

Another important finite element paper that investigates the link between paramasticatory loading and craniofacial morphology is that of Wang et al (2010). In this study they tested an FE model of a macaque skull in the scenario of paramasticatory loading. Unlike most studies, they tested multiple behaviours, moving the bite from incisor to premolars and molars, and also tested an anterior pulling force to simulate the behaviour of a bite with a manual pull (for example, stripping plant material). They found that midfacial prognathism did not help the model to resist the forces much better than the more orthognathic models when an anterior pull was also present, suggesting that frequent or forceful anterior pulling behaviours would not be likely to cause prognathic adaptation.

The testing of paramasticatory loading on finite element models is often used for the purpose of testing morphology related hypotheses. Palaeoanthropologists use finite element modelling to decipher relationships between behaviours identified in the archaeological record and the associated fossil hominin. One of the most infamous being Neanderthal craniofacial adaptations to paramasticatory loading, also known as the Anterior Dental Loading Hypothesis (Clement et al., 2012).

2.7 Fossil Hominid Functional Morphology

There are currently over 6000 individual hominids represented in the fossil record (Hawks, 2017), and they all represent approximately 20 hominid species (Plackett, 2021). Whether preserved as nearly complete skeletons or isolated bone fragments, each specimen provides valuable insights into the morphology, behaviour, and environmental adaptations of our extinct relatives. Functional morphologists investigate these fossils to best understand the causes for their unique morphologies using methods such as FEA, coupled with archaeological evidence for causational behaviours, however, a lot of results are open to interpretation leading to many debates (Daegling, 2022).

The *Australopithecus sediba* is a species that is subject to debate with regards to its relationship to the genus *Homo*, many argue that it is a transitional species due to its unique combination of ape like brain size and long arms, and more human like face and pelvis

(Williams et al., 2021). To functional morphologists these features would suggest that it was well adapted for both tree climbing/locomotion, but also walking upright (Berger, 2012). However, some argue that this may not be the case and that *A. sediba* has no relation to *Homo*, representing a separate lineage (Mongle et al., 2023). Ledogar et al (2015) investigated *A. sediba's* functional anatomy with regards to dietary adaptations, they found limited bite force capabilities which by their interpretations meant that *A. sediba* was better adapted to a softer diet. They claimed *A. sediba* shares biomechanical constraints with early *Homo* in this regard, which they believe strengthens the argument that they were a transitional species but insist that phylogenetic research will provide further insight as to whether this is the case, or if these traits have evolved in parallel.

Fig 2.17: Comparison of female *Homo sapiens* (left), *Australopithecus sediba* (centre), and male *Pan troglodytes* (right).
(Glandelle, 2013).

Another debate among functional morphologists is the nature of the "facial pillars" seen in the alveolar region (from canine to nasal aperture) of *Australopithecus africanus*. The most popular theory for their functional significance is that they developed to help the face resist the forces of mastication due to a hard food diet (Rak, 1985). However, research by

Strait et al (2009) used finite element models to assess this claim and found that they were more likely adapted to deal with the specific behaviours of premolar biting, this is linked with tough nuts and seeds cracking rather than a generally hard diet of raw meat and plant materials. Often the "facial pillars" are discussed as a shared characteristic with *Paranthropus robustus*, however, some researchers have argued that they are more likely a product of parallel evolution because the internal structures of these pillars are quite different, as the *P. robustus* pillars are full of trabecular bone rather than being hollow cortical bone like those of *A. africanus* (Villmoare & Kimbel, 2011).

Fig 2.18: Illustration of the skull of *Australopithecus africanus* specimen Sts5.
(Grine, 2013, p. 83, fig. 6.3).

There are several distinct craniofacial features that are shared amongst hominin, which when combined in a specific way, create the unique morphology of *Homo neanderthalensis*. The Anterior Dental Loading Hypothesis (ADLH) is the most prominent argument for the high degree of expression of these morphologies in Neanderthals compared to other species of *Homo*. It argues that the unusual make-up of the Neanderthal craniofacial region is due to adaptations to the heavy and frequent use of the anterior teeth as tools for daily activities (Clement et al., 2012). Although some of these traits can be seen in modern humans due to "a combination of archaic admixture and the retention of ancestral hominid traits", the magnitude in which these characteristics are presented varies widely (Sawyer & Maley, 2005).

Comparative studies have shown that anterior dental loading is not exclusive to Neanderthals. For instance, research on *Paranthropus boisei* and *Australopithecus africanus* has revealed robust craniofacial morphologies and dental microwear patterns consistent with high bite forces and potential paramasticatory behaviours, though these species exhibit different adaptive configurations than Neanderthals (Haywood, 2019). Similarly, extant primates such as Japanese macaques (*Macaca fuscata*) and Old World monkeys like *Cercocebus torquatus atys* demonstrate craniofacial strain patterns and dental topographies that reflect adaptations to habitual anterior loading, particularly in species that engage in behaviours like seed cracking or bark stripping (Antón, 1993; Ungar & Bunn, 2009).

There are a number of features that are being argued as having adapted to the forces caused by excessive dental loading, this includes distinctive features of dentition such as shovelling of incisors, crown size, root dimensions, and retromolar space. Microwear on the labial surfaces of incisors and canines, and macrowear of anterior dental crowns are commonly researched identifiers of dental loading that are used to determine the presence of paramasticatory activities that could have led to these adaptations. Other craniofacial features that are thought to be caused by anterior dental loading include; receding frontal squama, posteriorly bulging occipital region, tubercle on the mastoid process adjacent to the external auditory meatus, projecting midface, minimally angled zygomatic bone, retromolar space, and large coronoid process (Weaver, 2009).

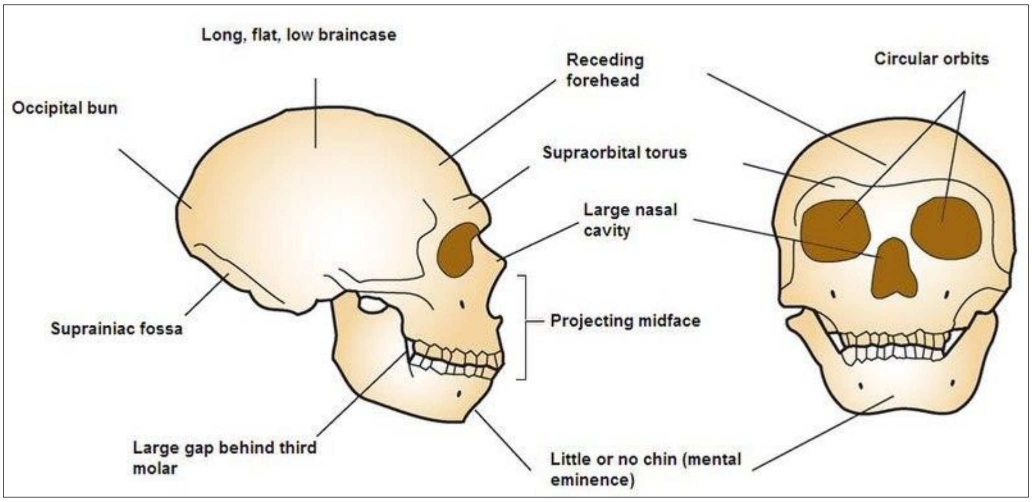

Fig 2.19: Diagram of Neanderthal craniofacial features (Potter, CC-BY-SA-2.5, 2006).

A great deal of research has focused on testing anterior dental wear in order to confirm whether paramasticatory behaviour was in fact present in Neanderthals - in such a way that would encourage their unique combination of craniofacial adaptations (Clement et al., 2008; 2012; 2015; Fiorenza et al., 2011; 2019; 2020; Hlusko et al., 2013). An important piece of research on Neanderthal macrowear is the 2012 paper published by Clement et al, where they created "dentine proportions" from measurements of exposed occlusal dentine from digital images of Neanderthals and other *Homo* specimens. Their results demonstrated that Neanderthal anterior dentition showed signs of heavier wear than their posterior teeth, thus supporting the idea that Neanderthals were performing paramasticatory activities. Research from KL Krueger took these ideas one step further by determining not only the presence of dental loading, but distinguishing paramasticatory activity from dietary in the patterns of microwear (Krueger, 2011; 2015; Krueger & Ungar, 2012; Krueger et al., 2013; 2017; 2019). Although the results from both authors supported that Neanderthals were loading their anterior dentition for behaviours other than mastication, they showed that other *Homo* species were also performing these behaviours but were not showing the same presentation of morphological adaptations and consequently rejected the hypothesis.

Although dental wear methods have rejected the ADLH, there have been many studies conducted on the various suspected morphological adaptations. One of these methods investigates the position of the muscles of mastication and their impact on mechanical advantage for producing bite forces on anterior teeth (Spencer & Demes, 1993). These findings gave support to the hypothesis that the Neanderthal craniofacial region was well adapted to the high biomechanical stresses expected from frequent heavy anterior dental loading. However, similar biomechanical modelling has been applied to other primates, such as *Cebus apella*, where postnatal heterochrony in masticatory apparatus development has been linked to dietary toughness and anterior bite force demands (Cole, 1992). These comparative models help contextualize Neanderthal adaptations within a broader evolutionary framework. Whilst the Spencer & Demes study was generally well received at the time of publishing, in more recent years the methods and findings have been questioned, with more recent conclusions contradicting their findings (O'Connor et al., 2005; Wroe et al., 2018). One of the most notable issues with their method is that only cranial material was measured, meaning that mandible measurements were not accounted for and thus approximations were used. As well as this, only one cranial measurement was used to assess muscle positioning, reducing the reliability of their analysis of the Neanderthal masticatory system (O'Connor et al., 2005).

A prominent Neanderthal finite element study is that of Wroe et al (2018), they looked into multiple hypotheses for the Neanderthal craniofacial region in order to understand whether they were adapted to; condition cold/dry air more effectively, facilitate greater ventilatory demands, or to paramasticatory loading. They investigated this using computational fluid dynamics (CFD) and finite element analysis (FEA). When combining their findings from FEA and CFD, they determined that Neanderthals were not clearly more adapted to frequent heavy anterior dental loading when compared to other *Homo* species, but that their facial morphology was better adapted for the cold as well as high energy demands. The particular process outlined in Wroe's study has proved to be popular in wider applications, being cited in multiple studies on the biomechanical adaptations of multiple species in the animal kingdom, both past and present (Galway-Witham et al., 2019; Tsang et al., 2019; Wang et al., 2019; Bicknell et al., 2022).

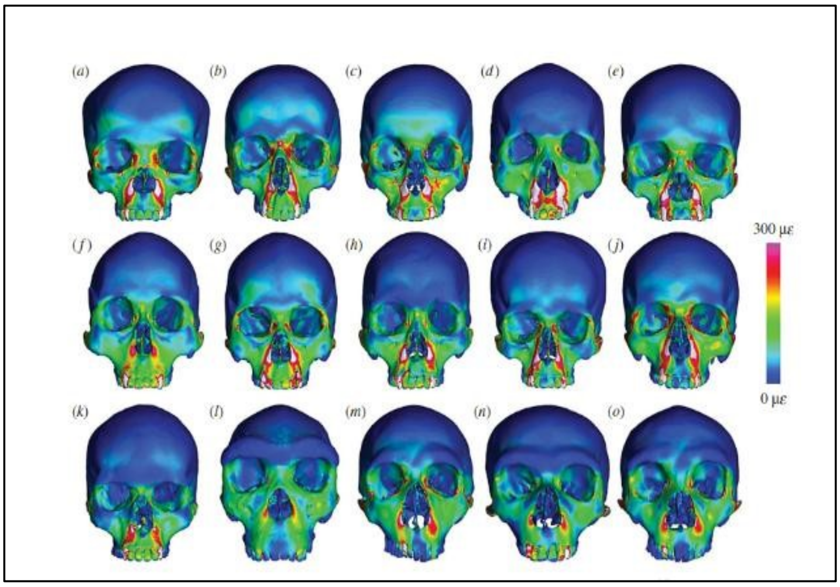

Fig 2.20: Comparative finite element analysis results of Von Mises micro-strains for a sample of various *Homo* specimens (Wroe et al., 2018, p. 04, fig. 2).

Due to the increasing popularity of FEA in biomechanical areas of research such as the craniofacial adaptations of Neanderthals, great care must be taken to ensure that the methods and results being published are both reliable and accurate. FEA validation studies have been published in recent years aiming to discern the methods accuracy, sensitivity, and the future of FEA (Bright & Rayfield, 2011; Toro-Ibacache et al., 2016; Godinho et al., 2017). Using both real and predictive methods for determining the amount of strain, studies such as that of Godinho et al (2017), have found that it is possible to test how accurately FEA will portray the strains and deformations of the cranium during specific loading scenarios. The results of this particular study demonstrated that whilst craniofacial FEA is useful for predicting the general spatial pattern of strain, it is not entirely accurate when predicting fine local variations, magnitudes, and directions. Rather than suggesting the issue is with FE modelling itself, studies such as Godinho's suggest that higher resolution scans could improve the accuracy of the method.

Research on other hominid species has further highlighted the importance of methodological precision. For instance, FEA applied to *Homo floresiensis* revealed strain magnitudes resembling those of modern humans, suggesting a reduction in high-force biting behaviours relative to other Australopiths (Cook et al., 2021). These findings imply that even small-bodied hominins with robust cranial features may not have heavily relied on high-force mastication, complicating assumptions about craniofacial adaptation across the genus *Homo*. Similarly, comparative FEA across fossil hominins has demonstrated that differences in craniofacial form can yield contrasting mechanical outcomes depending on how muscle forces and bite scenarios are scaled (O'Higgins et al, 2017; Mitchell et al, 2025). These studies highlight the need for standardised and ecologically relevant loading conditions when interpreting functional morphology.

Another issue that is overlooked in hominid FEA models is that only one biting behaviour has been tested - a vertical bilateral incisor bite. Testing various loading behaviours (including anterior pulls) may change the way in which the craniofacial strain patterns are displayed, thus potentially changing the conclusions that are drawn on the plausibility of hypotheses like the ADLH. Including behaviours such as clamping and pulling on an item, and changing gapes may show different patterns to the regular chewing motion which may highlight varying strain scenarios in the craniofacial region depending on which behaviour is being carried out. Knowing that some hominin populations lived in cold environments and may have performed habitual behaviours such as hide scraping more frequently (Cheesman, 2021), it is a possibility that when loading a model with this behaviour, it may show that their adaptations were for paramasticatory behaviours such as this, rather than a standard bilateral incisor bite.

A further issue with FEA that studies such as Godinho et al's (2017) do not appear to have picked up on, is that only the muscles of mastication are included in these models. When testing anterior dental loading *in vivo* muscle activation is only monitored for the muscles of mastication (Spencer, 1998; Richmond et al., 2005; Toro-Ibacache & O'Higgins, 2016), this is then replicated in computational simulations and *in vitro* testing (Kupczik et al., 2009; Toro-Ibacache et al., 2016; Godinho et al., 2017). When considering the vital role that neck muscles play in head stabilisation, their inclusion in craniofacial testing seems to be an obvious choice, however while it is common to see their inclusion in palaeontological and medical research (Rayfield et al., 2007; Snively & Russell, 2007; Hellmann et al., 2012; Giannakopoulos et al., 2013) they are not seen in any craniofacial testing related to the anterior dental loading hypothesis, whether it be *in vivo* or virtual experimentation. The complete exclusion of neck muscles in this avenue of research may prove to be an issue, as the stabilisation of the head and potential aid to the masticatory muscles, could have an effect on the overall strain patterns produced in the craniofacial region, thus perhaps calling into question the current understanding of hominid craniofacial functional morphology.

2.8 Summary

The use of finite element analysis (FEA) to explore craniofacial form and function in fossil hominins has grown substantially over the past two decades. A wide range of studies have examined how variables such as masticatory muscle forces (Ross et al., 2005; Shi et al., 2012) and bite location (Fitton et al., 2012; Panagiotopoulou et al., 2017) influence strain patterns across the craniofacial skeleton. Building on this foundation, researchers have begun to investigate the biomechanical implications of paramasticatory behaviours, which remain underexplored in comparative models.

Despite progress, many existing FEA studies rely on simplified cranial models that exclude key anatomical components, such as neck musculature, and typically simulate only a narrow range of static bite behaviours. One notable gap is the lack of modelling for anterior pulling forces, which may be biomechanically significant in a variety of habitual behaviours across hominin taxa. The omission of such behaviours limits our understanding of how craniofacial structures respond to diverse loading scenarios.

This thesis aims to refine current modelling approaches by incorporating neck extensor musculature and simulating a broader spectrum of anterior dental loading behaviours, including pulling and clamping actions. Drawing on established methodologies from craniofacial biomechanics, palaeontology, and biomedical engineering, the project will assess whether a more anatomically complete and behaviourally realistic framework alters interpretations of craniofacial strain. The findings will contribute to wider discussions on the functional morphology of fossil hominins and the potential adaptive significance of anterior dental use beyond mastication.

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Research Degree Thesis Statement of Authorship

Note that where a paper has multiple authors, the statement of authorship can focus on the key contributing/corresponding authors.

Candidate name	Lauren Spencer
Department	Archaeology
Thesis title	Simulation of Anterior Biting Behaviours: Surface EMG and Strain Mapping of Craniofacial Responses

Title of the work (paper/chapter)	Creating a Finite Element (FE) Model Suitable for Anterior Dental Loading Behavioural Testing	
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Description of the candidate's contribution to the work*	Responsible for the development and execution of the study, including finalising the research design, constructing and testing the finite element models, analysing the results, and writing the chapter.
Approximate percentage contribution of the candidate to the work (*if possible to describe in this way*)	90%

Signature of the candidate	**Lauren Spencer**
Date (DD/MM/YY)	**03/11/2025**

Co-author contributions

By signing this Statement of Authorship, each co-author agrees that:

(i) the candidate has accurately represented their contribution to the work;

(ii) if required, permission is granted for the candidate to include the work in their thesis (note that this is separate from copyright considerations).

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Approximate percentage contribution of the co-author to the work (*if possible to describe in this way*)	10%
Signature of the co-author	
Date (DD/MM/YY)	03/11/25

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*The description of the candidate and co-authors contribution to the work may be framed in a manner appropriate to the area of research but should always include reference to key elements (e.g. for laboratory-based research this might include formulation of ideas, design of methodology, experimental work, data analysis and presentation, writing). Candidates and co-authors may find it helpful to consider the [CRediT (Contributor Roles Taxonomy)] approach to recognising individual author contributions.

Chapter 3: Creating a Finite Element (FE) Model Suitable for Anterior Dental Loading Behavioural Testing

Lauren Spencer; Laura Fitton.

Written as for publication but not for submission.

Abstract: Finite element analysis (FEA) has become an increasingly important tool for investigating the effects of cranial loading on craniofacial strain and, by extension, for inferring dietary behaviour and morphological variation in both extant and fossil taxa. Given its value in paleoanthropological research, it is essential that models replicate realistic loading scenarios that reflect feeding behaviour as accurately as possible. Most published FE models to date, however, examine only a single loading behaviour (typically a vertical bite) and rarely, if ever, include the neck musculature. These omissions may result in unrealistic strain predictions and potentially misleading interpretations.

This chapter therefore investigates, through sensitivity analysis, the effects of varying bite loading conditions and the inclusion of neck musculature on craniofacial strain. Boundary conditions were systematically tested to assess the influence of temporomandibular joint and occipital condyle constraints, as well as the addition of anteriorly directed forces. Four neck extensor muscles (sternocleidomastoid, splenius capitis, semispinalis capitis, and upper trapezius) were incorporated individually and collectively to examine their potential mechanical impact.

The results indicate that variations in constraint placement produced only minor, localised effects on strain magnitude and distribution, whereas inclusion of the neck extensors had a global impact on both. Muscles attaching to the mastoid region produced similar strain patterns, whereas those inserting into the nuchal region generated distinct effects. These findings demonstrate that the neck musculature substantially influences craniofacial strain and should be considered when modelling anterior biting. The optimised model developed here forms the foundation for further analyses in Chapter 4.

3.1 Introduction

A critical step in testing biomechanical hypotheses, such as the Anterior Dental Loading Hypothesis (ADLH) or broader questions about dietary impacts on craniofacial strain, is constructing accurate finite element (FE) models. While FE modelling has been used in ADLH research (Wroe et al., 2018) many studies rely on simplified, or in some cases inappropriate, loading conditions that may fail to capture the full complexity of craniofacial biomechanics (O'Connor et al., 2005; O'Higgins et al., 2019; Genochio, 2022). As a result, some interpretations of craniofacial strain may be misleading or incomplete (Toro-Ibacache et al., 2016a; Godinho et al., 2017).

This chapter seeks to address these methodological gaps by constructing detailed FE models of the human cranium and assessing the influence of factors commonly excluded from previous ADLH studies. It examines the effects of anterior pulling forces on the incisors and the contraction of neck extensor muscles, which are likely to be active during anterior dental loading (Hellmann et al., 2012; Giannakopoulos et al., 2013a; 2013b; 2018; Im et al., 2015). Neck muscles have already been shown in non-primate species to contribute significantly to craniofacial strain patterns in finite element models (McHenry et al., 2007; Snively & Russell., 2007; Hellmann et al., 2012; Wroe et al., 2013; Figueirido et al., 2018), but little is known of their role in humans.

Specifically, this chapter outlines the creation of male and female FE models from CT data, describes the use of virtual modelling software for segmentation and simulation (Kupczik et al., 2009; Gröning et al., 2011) and outlines a plan for a series of sensitivity tests to evaluate model responses under varying constraint and loading conditions. This includes the novel inclusion of neck extensor muscles and occipital condyle constraints, elements not currently incorporated into ADLH or feeding models (Stansfield et al., 2018; Stelzer et al., 2018; Wroe et al., 2018; Krueger et al., 2019; Lacruz et al., 2019). By systematically evaluating how these parameters alter strain distributions, the chapter aims to develop a biomechanical model better suited to isolating the specific effects of anterior loading behaviours on craniofacial form.

These refined models will then provide the methodological foundation for the analyses presented in Chapter 4, supporting a more nuanced investigation into how anterior dental loading influences craniofacial strain.

3.1.1 Overview of FEA in Craniofacial Biomechanical Modelling

Finite element analysis (FEA) originated in the 1940s and 1950s as a method for solving complex structural engineering problems (e.g. Hrennikof, 1941; Argyris, 1954; Turner et al., 1956). The term "finite element method" was coined by Clough (1960), and the technique quickly spread across engineering disciplines and, eventually, into biomedical sciences

(Clough & Wilson, 1999). By the 1970s, FEA was being applied to human anatomy. In 1973, Farah et al. published one of the first FEA studies in dental biomechanics, modelling a single tooth. From there, the technique was extended to broader aspects of the masticatory system, including cranial biomechanics.

At a basic level, FEA involves four key inputs: a geometric model (typically from CT scans), material properties (e.g. isotropic vs. anisotropic bone), loading regimes (muscle forces or external forces), and constraints (e.g. joints or bite points). The output is a spatially resolved prediction of mechanical performance, usually reported as stress, strain, or displacement fields. Though simple in concept, how each of these variables is defined, and how biologically accurate those definitions are, has been an enduring challenge in cranial biomechanics (King, 1984; Korioth & Versluis, 1997; Wong et al., 2011; Parashar & Sharma, 2016).

The widespread use of FEA in palaeoanthropology and comparative cranial biomechanics took off in the early 2000s, led by a small group of researchers working across anatomy, palaeontology, and engineering. Among them were Emily Rayfield, Jen Bright, Elizabeth Dumont, Brian Richmond, Kornelius Kupczik, Paul O'Higgins, Laura Fitton, Stephen Wroe, Callum Ross, Phil Cox, David Strait, and Michael Berthaume (P. O'Higgins, 2000; EJ. Rayfield, 2004; Dumont et al., 2005; Richmond et al., 2005; CF. Ross, 2005; Wroe et al., 2007; PG. Cox, 2008; Kupczik et al., 2009; Strait et al., 2009; Berthaume et al., 2010; Bright & Rayfield, 2011a; Fitton et al., 2012). These researchers helped develop the methodological foundations of cranial FEA, each working with different software (e.g. Strand7, ABAQUS, ANSYS, Vox-FE), workflows, and biological systems.

Their work was exploratory, pioneering, but by necessity, inconsistent, with different teams wrestling with core questions: How should cranial models be segmented and meshed? (Autuori et al., 2005; Bright & Rayfield, 2011a) What material properties best represent cranial or dental tissues? (Strait et al., 2005; Wang et al., 2006) How much force should muscles exert? Should it reflect the muscles' Physiological cross-sectional area? Intrinsic strength? EMG activation? (Ross et al., 2005; Bright & Rayfield, 2011b; Fitton et al., 2012) Where should models be constrained, and how do those choices affect the results? (Stansfield et al., 2018) How can one interpret results across individuals, species or fragmentary fossils? (S. Wroe, 2008; Dumont et al., 2009).

Early on, it became clear that FEA could be used to ask evolutionary questions, but also that methodological decisions had profound effects on the outcome. Validation and sensitivity studies emerged as a response: attempts to test how robust FEA predictions were under small changes in input. Validation experiments often compared FEA predictions to real strain data collected *ex vivo* (e.g. on human or macaque cadaver skulls) (Toro-Ibacache et al., 2016b; Godinho et al., 2017) or *in vivo* (in macaques with implanted strain gauges) (Ross et al., 2011; Panagiotopoulou et al., 2017). But these setups were imperfect, *in vivo* animals were artificially constrained to prevent excess movement and the pulling out of strain gauges, as explained in a 2011 study by Ross et al, which placed strain gauges on the postorbital bar of four rhesus macaques "[They] were placed in a commercially available restraint (XPL-517-CM; Plas Labs, Lansing, MI, USA) that restrained an animal's arms while enabling the head and neck to move freely".

In addition to this, *ex vivo* loading was simulated and modelled, but often did not match natural feeding conditions, as seen in a 2016 study by Toro-Ibacache et al, in which the skeletonised head of a 74-year-old man was compressed from above whilst being supported below by steel blocks (see figure 3.01). Although a reaction force would be detected as the left incisor makes contact with the load cell the compressive force would instead be coming from below (the mandible) in a real-life scenario. As such, it is possible models could match measured strains under artificial conditions, but there was no guarantee they mimicked real masticatory loading, especially ones which used more extreme stripping or paramasticatory behaviours (see Chapter 2).

Fig 3.01: Image of the experimental set up for strain measurement; vertical compressive load applied to the calvarium (upper arrow) simulating a left central incisor bite (lower arrow). The asterisk shows the DSPI sensor attached to the infraorbital region (Toro-Ibacache et al., 2016, p. 72, fig 1).

Sensitivity studies, in turn, showed that variables like bite point, muscle activation pattern, and constraint location all had substantial effects on predicted strain (Ross et al., 2005; Fitton et al., 2012). Stansfield et al (2018) published a study that performed four sensitivity tests which concluded that varied material properties, muscle vector orientations, and location of constraint on the biting tooth and condyles, had less effect than change in mandible form (segmented CT scans from nine individuals). Researchers explored ways to refine muscle estimates, including multibody dynamics models (Shi et al., 2012) and cross-species extrapolations from primate EMG data (Smith et al., 2021; Haravu et al., 2022; Panagiotopoulou et al., 2023). But in most cases, the lesson was one of caution: model outputs are only as reliable as the assumptions behind them.

One particularly unresolved issue was how best to constrain cranial models. Reactions during feeding can be distributed across several anatomical points: the mandibular condyles, the bite point, and potentially, the occipital condyles. Early work by researchers such as Panagiotopoulou (2009), and Bright and Rayfield (2011) questioned how different constraint combinations might affect model output. Most studies eventually adopted a simplified protocol using just the temporomandibular joints (sometimes also the bite point), based on the assumption and findings that occipital condyles would increase the risk of over-constraining the model and have little valid effect on strains (personal communication with Laura Fitton). This made sense given their anatomical location, alignment with muscle vectors, and the fact that validation studies produced reasonable strain fields without including them (Ross et al., 2005; Godinho et al., 2017). To date, no hominin FEA model includes an occipital condyle constraint, and this has become standard practice.

However, there are reasons to question whether this is always valid. Consider a scenario in which posterior neck muscles contract to pull the skull backwards (e.g. looking up). In such cases, the occipital condyles act as a pivot point and may generate reaction forces. If these forces are excluded, strain distributions may be incorrectly estimated. This raises the broader issue of neck musculature, which is also routinely excluded from FEA models of feeding.

In fact, neck muscles are never included in FEA studies of feeding in hominins or extant mammals. Some dinosaur studies such as that by Snively and Russell (2007) have evaluated the functional impact of neck muscles and concluded that neck musculature could significantly influence cranial strain patterns, leading to their inclusion in later studies like that of Button et al (2014), which modelled neck muscles in their investigation of sauropod cranial biomechanics. In humans, clinical biomechanics and EMG studies show that neck muscles activate during biting, chewing, and head stabilisation (Ciuffolo et al., 2005; Tecco et al., 2007; Tartaglia et al., 2008). Work by Hellmann et al (2012) expanded on previous EMG studies which relied exclusively on the sternocleidomastoid and the trapezius muscles and discovered that multiple anterior and posterior neck muscles co-contract with the muscles of mastication during a variety of chewing and clenching tasks, even when no neck movement was required, this was supported in subsequent works by Giannakopoulos (2013a; 2013b; 2018). In behaviours that pull on the skull, such as tugging or tearing, neck extensors are likely to contract to counteract head flexion. If so, their exclusion from FEA models may remove an important component of loading, especially if paramasticatory forces are being investigated.

Directionality of loading also matters. Most FEA models simulate vertical loading at bite points, but some studies (e.g. Wang et al., 2010; Benazzi et al., 2015; McCurry et al., 2015) have tested the impact of anterior pulls on teeth. These produce different strain distributions, with important implications for anterior dental loading scenarios. For example, anterior pulling forces may place greater strain on the midface in particular, altering interpretations of mechanical adaptation (Wang et al., 2010).

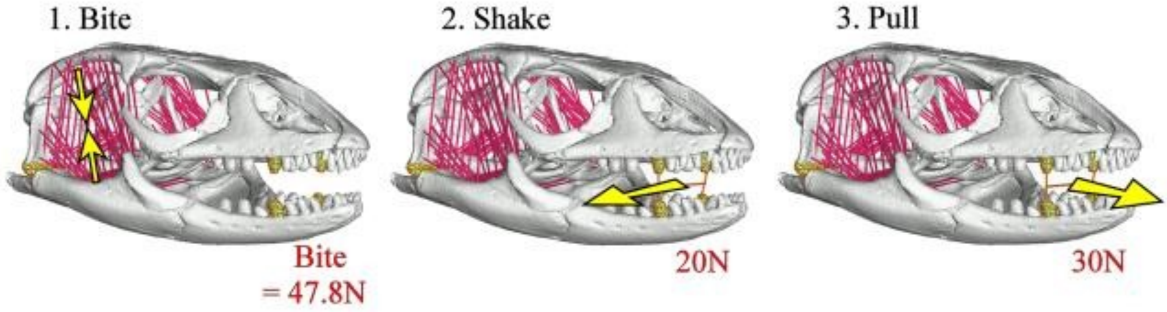

Fig 3.02: Diagram showing the three behavioural load cases tested on a finite element model of a *Varanus exanthematicus* specimen; 1. Bite at middle teeth 2. Bite and lateral pulling force at middle teeth 3. Bite and anterior pulling force at middle teeth (McCurry et al., 2015, p.7, fig. 3).

Despite these known limitations, FEA has been applied to major paleoanthropological debates, from australopith dietary adaptation (Strait et al., 2009; Smith et al., 2015; Ledogar et al., 2016) to the function of Homo heidelbergensis brow ridges (Godinho et al., 2018). Many models rely on simplified vertical biting loads, which may be acceptable for certain questions. But there has been concern for decades that models may be simulating stress under unrealistic behaviours (Grine et al., 2010), which risks producing compelling but misleading evolutionary interpretations.

This issue is especially relevant to the Anterior Dental Loading Hypothesis (ADLH). Recent studies have loaded fossil crania at the incisors to test whether Neanderthals or other hominins were better adapted to resist strain in this region (Wroe et al., 2018; Genochio, 2022) (see chapter two for further details around the ADLH). The assumption underlying many FEA studies is that habitual behaviours produce strain-adaptive craniofacial morphologies. However, as discussed, most models omit important biomechanical elements: neck musculature is excluded, occipital constraints are rarely applied, and loading is typically vertical rather than anterior. This raises an important question: Do these omissions meaningfully affect strain predictions, or are their effects negligible?

To address this question, this chapter systematically explores how strain outcomes vary when altering these previously under-studied inputs.

There are many ways to construct an FE model, and depending on the software used, different modelling approaches and assumptions are required. Choices vary from meshing strategies (e.g., polygonal tetrahedral meshes vs. voxel-based hexahedral meshes), to material property definitions (homogeneous isotropic bone vs. heterogeneous anisotropic bone), to how muscles are simulated (e.g., as simple linear elastic trusses versus more complex spring models). Each of these modelling decisions can substantially influence the resulting stress and strain predictions. Mesh density, element type, material assumptions, and the way forces are applied can all affect not only the magnitude but also the spatial distribution of strain (Bright & Rayfield, 2011; Gröning et al., 2013; Dumont et al., 2009). While software platforms impose certain constraints on model-building workflows, and these can have potential consequences, as long as all other variables are kept constant, it should still be possible to gain an understanding of the potential impact of anterior pulling, neck muscle loading, and occipital condyle constraints of the biological interpretation of craniofacial strain.

In this study, the available software was VOX-FE, a platform specifically designed to handle large-scale, high-resolution, voxel-based models derived from CT data. VOX-FE is particularly suited to bone and craniofacial biomechanics, where the original imaging data is voxel-based, and has been widely used in peer-reviewed FEA studies (e.g., Kupczik et al., 2009; Gröning et al., 2011; Fitton et al., 2012, 2015; Cox et al., 2013; Stansfield et al., 2018).

VOX-FE has also been extensively applied in studies focused on validation and sensitivity testing of both human and non-human crania (e.g., Fitton et al., 2012; Toro-Ibacache et al., 2016b; Godinho et al., 2017) and has proven to be a robust and flexible package. While some terminology and technical procedures in this chapter are specific to VOX-FE (e.g., voxel based meshing, constraint handling), the general biomechanical principles and sensitivity findings are expected to be broadly transferable across different FEA platforms.

In this study, Avizo Lite 9.2.0 was used for the initial stages of model preparation. Avizo is commonly employed in FEA workflows to convert computed tomography data into 3D digital models via segmentation (Hogg et al., 2011; Gurr et al., 2022; Najafzadeh et al., 2024). It also provides tools for measuring cross-sectional areas of muscles, calculating morphometric angles, and placing digital landmarks that can later be imported into VOX-FE to define muscle vectors.

To test the potential importance of loading parameters relevant to the Anterior Dental Loading Hypothesis (ADLH), a series of sensitivity analyses were conducted. Specifically, this chapter examines how model behaviour is affected by (1) the method of applying an anterior pull (including the surface area coverage of the incisal constraint and the anterior load), (2) the presence or absence of occipital condyle constraints, together with the position of the TMJ constraints, and 3) the inclusion of neck muscles.

The reason for these and the specifics are as follows: results from dental wear studies have indicated that incisal bite location/wear in Neanderthals was commonly centrally along the incisal ridge (O'Connor et al., 2005). When we consider how people load their FE models, the number of constrained nodes or pulling forces selected (and thus the surface area coverage) has varied substantially between FEA studies. Stansfield et al. (2018), for instance, constrained nearly twice as many nodes as Godinho et al. (2017), potentially influencing localised strain patterns. The effect of varying the area of constraint application is therefore explicitly tested in this study. Anterior pull forces are also examined. Pulling forces have been applied successfully in other species (Dinosaurs: Rayfield, 2004; Pollock et al., 2022; Macaques: Chalk et al., 2011), so this chapter investigates whether load placement (i.e. where on the tooth) or behaviour (which direction of pull) impact cranial strain the most.

Occipital condyles are rarely constrained in feeding models, likely due to the assumed absence of posterior muscle forces, but may play a stabilising role when posterior loads are present (Klenner et al., 2016). Their potential to alter strain distributions is tested here for the first time in a hominin-relevant context. The TMJ is another key constraint, and although the mandible itself is not included, correct constraint placement at the articular surface is essential for producing realistic joint reactions (Stansfield et al, 2018). Because joint position can vary with gape, its placement may influence strain near the midface and base of the cranium. A few studies have investigated kinematics on strain patterns but their work has been focused on mandibles and non-human species (McIntosh & Cox, 2016; Panagiotopoulou et al., 2023).

Finally, this study introduces neck musculature into the finite element model, an innovation for palaeontological FEA studies. Following protocols from both human EMG research and comparative finite element work (Snively & Russell, 2007; Hellmann et al., 2012;

Giannakopoulos et al., 2013), neck extensor muscle forces are estimated and applied (see chapter two for a full review of the neck musculature).

Neck musculature is rarely included in FEA models of cranial loading (Dumont et al., 2005; Bright & Rayfield, 2011; Fitton et al., 2012; Ledogar et al., 2016; Toro-Ibacache et al, 2016a), likely due to a combination of modelling complexity and the assumption that jaw adductors dominate strain production during feeding. In addition, empirical data on neck muscle activation during mastication, especially in non-human primates, remains limited. As a result, most studies exclude these muscles by default, a trend reinforced by the precedent set in earlier FEA work. However, this omission has rarely been tested systematically. This chapter addresses that gap by incorporating neck extensor forces and evaluating their impact on cranial strain predictions.

Given the validation work previously undertaken using VOX-FE (e.g. Toro-Ibacache, 2013; Godinho et al., 2017), and the goal of enabling useful interpretation of results in the context of hominin craniofacial evolution, it was deemed appropriate to use modern human crania for this study.

Together, these tests aim to clarify whether common modelling simplifications in feeding studies, such as omitting posterior constraints, simple vertical bite application, or omitting neck musculature, are negligible or whether they risk distorting the biomechanical signals used to reconstruct evolutionary and functional hypotheses. This work provides a methodological foundation for the comparative interpretations explored in subsequent chapters.

3.1.2 Chapter Aim and Hypotheses

<u>Aim</u>

The aim of this chapter is to determine the most appropriate approach for constructing finite element (FE) models capable of accurately predicting craniofacial strain patterns during masticatory and paramasticatory behaviours. Specifically, the study evaluates how variation in loading regimes, constraint strategies, and the inclusion of neck musculature affects model outcomes relevant to anterior dental loading.

Hypotheses

It is hypothesised that:

1. **Alterations** in the placement of temporomandibular joint (TMJ) constraints will affect strain magnitudes and distributions, particularly near the midface and cranial base.
2. The location of anterior pull forces applied to the incisors will significantly impact craniofacial strain outcomes.
3. The inclusion of occipital condyle constraints will primarily influence strain distributions at the cranial base but have minimal effects on midfacial strain during anterior loading.
4. The incorporation of neck extensor muscle forces will have a more global effect on craniofacial strain patterns, potentially altering both facial and cranial vault biomechanics, especially during anterior loading scenarios.

3.2 Materials and Methods

This section outlines the protocol for the selection of the modern human specimen, the segmentation of cranial bone and dentition from a CT scan (.dcm), and the procedures used to reorient the model into an anatomically realistic head posture suitable for simulating masticatory and anterior dental loading. The preparation of finite element (FE) model is then described, including the application of boundary conditions, loading regimes, and muscle force vectors necessary for subsequent biomechanical analyses.

3.2.1 Specimen Selection

One adult human individual was selected from the New Mexico Decedent Image Database (NMDID) to serve as the basis for model construction. Selection criteria included: (i) age between 20–30 years, (ii) complete permanent dentition in good condition, (iii) absence of craniofacial trauma, and (iv) high-quality CT scan of both the skull and upper thorax. The selected specimen was a 20-year-old Native American female. Following access approval, the DICOM image stacks (.dcm) were downloaded and imported into Avizo Lite (version 9.2.0) for processing. The medical CT scan was at a resolution of 0.43 x 0.51 x 0.61mm.

Fig 3.03: Volume rendering (.am) of female specimen in the lateral view in Avizo Lite 9.2.0 (opacity setting: 0.15%).

3.2.2 Image Segmentation and Model Preparation

CT data of the specimen was segmented in Avizo using a two-stage process. An initial global threshold was applied to isolate high-density structures (bone and teeth), followed by manual segmentation to separate the cranium, mandible, maxillary teeth, and upper cervical spine (figure 3.04). Particular attention was paid to avoid contact between the dentition. Floating voxels (i.e., disconnected elements) were identified and removed. Fine segmentation of delicate cranial structures (e.g., internal nasal conchae, orbital bones) was performed using a lower grey-scale threshold and manual editing (figure 3.05). This process left four individual materials; the cranium, maxillary teeth, the mandible, and the thorax which were then converted from a volume rendering to a surface file (.surf).

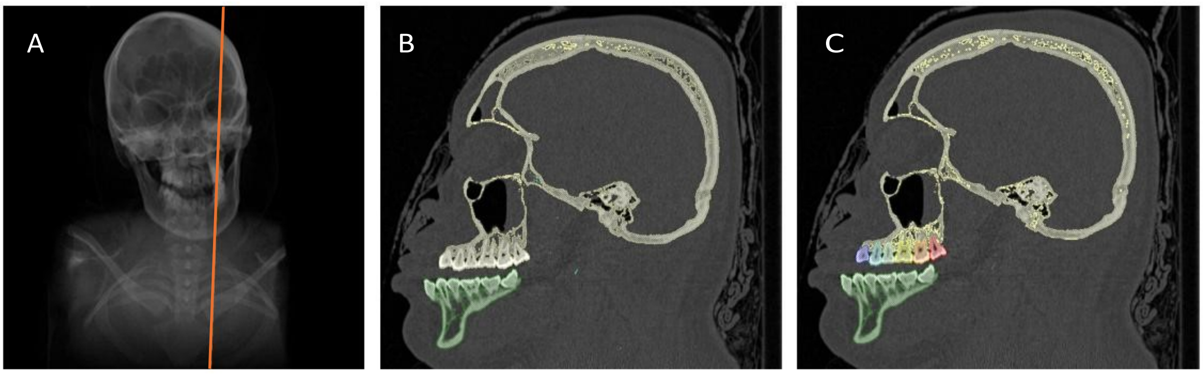

Fig 3.04: Sagittal section through the skull showcasing the process of segmentation for the female specimen. a) Volume rendering (.am) of the specimen with ortho slice 352 oriented in sagittal plane b) Initial thresholding segmentation: Mandible shown in green, cranium and maxillary dentition shown in yellow. Note that the teeth are not separated from the surrounding bone. C) Manual segmentation: Maxillary teeth have now been individually segmented (each tooth now highlighted in its own colour).

Fig 3.05: Coronal section through the skull showcasing the process of segmentation for more delicate bone of female specimen. a) Volume rendering (.am) of the specimen with ortho slice 115 oriented in coronal plane b) Threshold re-segmentation: new, lower grey threshold shown in blue, cranium shown in yellow, mandible shown in green. c) Manual segmentation: lower threshold segmentation leaves some material behind, so manual segmentation was used to segment individual voxels that were

3.2.3 Model Alignment

As shown below in Figure 3.06, the skull and thorax were not in standard anatomical position due to the cadaver having been scanned in a supine (horizontal) posture. The head also exhibited a degree of extension relative to the cervical spine, resulting in a cranio-cervical relationship that did not correspond to an upright anatomical posture. Additionally, the segmented model was positioned outside the positive region of the global coordinate system.

To correct this, the segmented models were reoriented using the Frankfurt Plane as a reference (Figure 3.06). The Frankfurt Plane, defined by the inferior margin of the orbit and the superior margin of the external auditory meatus, was aligned parallel to the XZ plane to standardise cranial orientation. As VOX-FE is orientation-dependent, consistent alignment with anatomical planes is critical for model stability and comparability.
The skull was translated so that the right atlanto-occipital joint was positioned at the global origin (0,0,0) and then rotated to align the Frankfurt Plane horizontally.

The cranio-cervical relationship was corrected following the protocol of Fonseca et al. (2013) Landmarks were placed along the Frankfurt Plane (on the cranium) and on the posterosuperior surface of the odontoid process and the base of the C4 vertebra (Figure 3.06). The intermediate angle ('a') was measured to calculate the desired cranio-cervical inclination angle ('b'). The cervical vertebrae were rotated through the occipital condyles until an inclination of 85.2° was achieved, matching the average reported by Fonseca et al. (2013).

Finally, the entire model was translated into positive XYZ space to conform with the global coordinate requirements of VOX-FE.

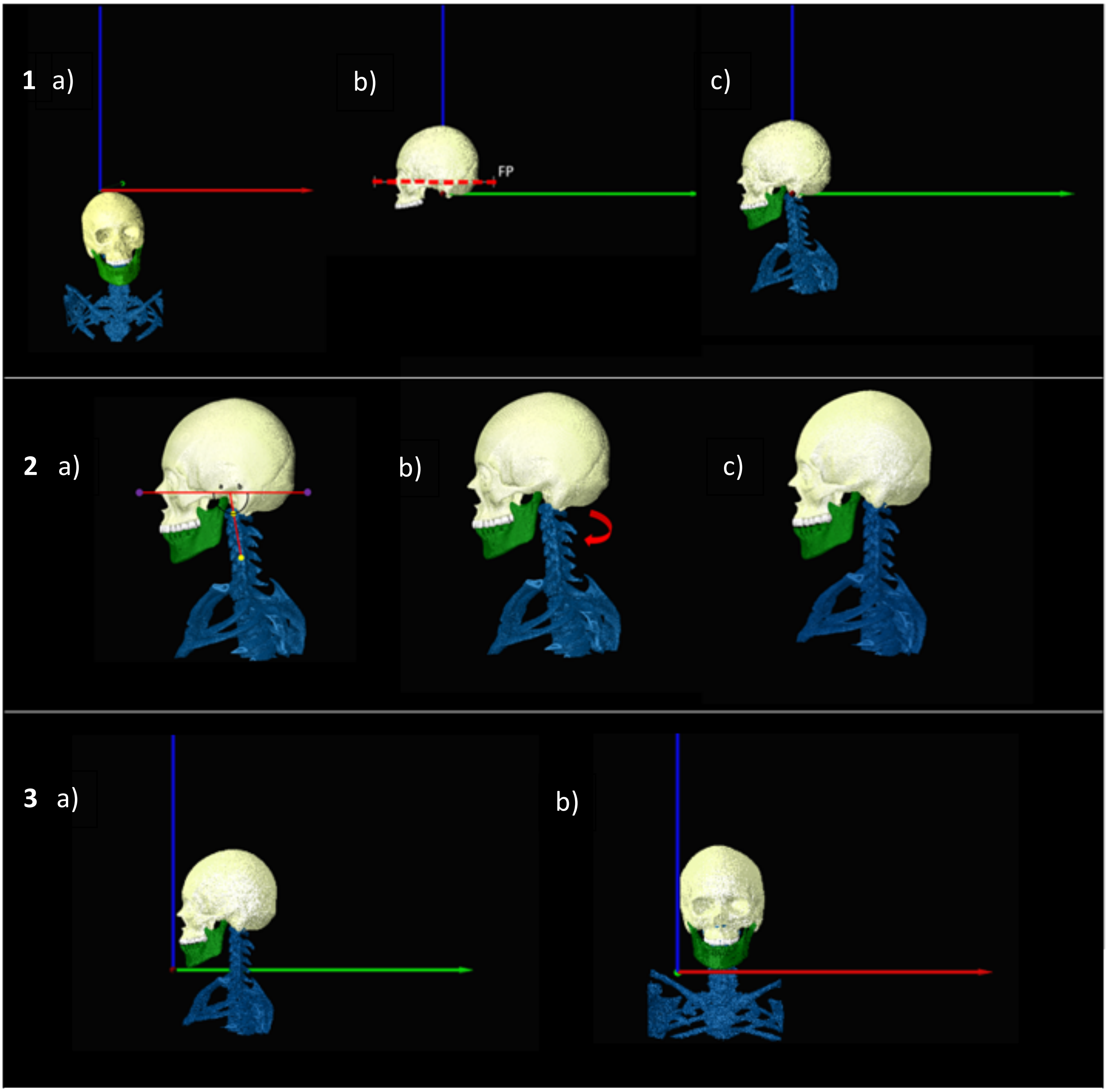

Figure 3.06: Full process of transforming, translating, and aligning model. 1a) Original position of the model (.surf), demonstrating that the Frankfurt Plane (FP) of the model is not aligned with the X or Z axes and lies outside of the positive region of the global coordinate system. 1b) Reorientation of the skull (yellow) so that the FP is parallel to the XZ plane. 1c) Rearticulation of the mandible (green), cervical vertebrae and thoracic skeleton (blue) to align correctly with the reoriented skull (yellow). 2a) To create a more standard anatomical position landmarks were placed along the FP of the skull (purple), and spinal landmarks (yellow) in order to measure the cranio-cervical inclination. 2b) Using angle 'b' the cervical vertebrae and thoracic skeleton were then rotated through the occipital condyles. 2c) The fully segmented model is now correctly articulated and aligned. 3a) Sagittal view of the final positioning of the model after transformation, translation, and alignment. 3b) Frontal view of the final positioning of the model after transformation, translation, and alignment.

3.2.4 Landmarking Muscle Origins and Insertions

3.2.4.1 Masticatory Muscles

Once the skeletal elements of the model were prepared, the next stage involved landmarking (.landmarkAscii) the main muscles of mastication. Origin and insertion points were manually placed on the skull and mandible in Avizo to define muscle force vectors for subsequent application in VOX-FE. In Figure 3.07, the temporalis muscle landmarks (brown) can be seen placed on the temporal fossa and the coronoid process of the mandible. Masseter landmarks (orange) were placed on the inferior surface of the zygomatic arch and the lateral surface of the mandibular ramus. The medial pterygoid landmarks (blue) were located on the medial surface of the lateral pterygoid plate of the sphenoid bone and the medial surface of the mandibular ramus.

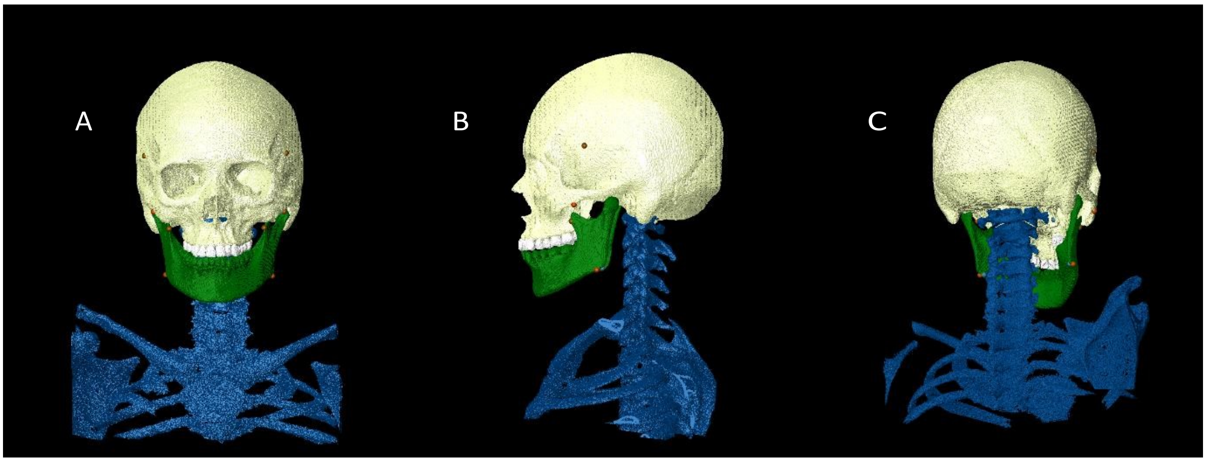

Fig 3.07: Placement of landmarks for the masticatory muscles. a) Frontal view of the origins and insertions. b) Lateral view of the origins and insertions. c) Rear view of the origins and insertions.

3.2.4.2 Neck Extensor Muscles

Following the same approach used for the masticatory muscles, the origin and insertion points for selected neck extensor muscles were also landmarked in Avizo (.landmarkAscii). These included the sternocleidomastoid, trapezius pars descendens, semispinalis capitis, and splenius capitis. Unlike the masticatory muscles, the neck extensors originate on elements of the thorax and cervical spine, which lie in negative coordinate space relative to the cranial model. Therefore, after landmarking, midpoints between origin and insertion landmarks were calculated to define accurate force vectors in VOX-FE, following the protocol described by Van der Horst (2002).

The landmarked attachments are illustrated in Figure 3.08: Sternocleidomastoid (red): from the superior anterior surface of the manubrium sterni to the mastoid process of the temporal bone. Trapezius pars descendens (yellow): from the lateral third of the clavicle to the superior nuchal line of the occipital bone. Semispinalis capitis (white): from the articular processes of C7 (midpoint between superior and inferior origins) to a point just below the superior nuchal line. Splenius capitis (pink): from the nuchal ligament at C6 (midpoint between superior and inferior origins) to the mastoid process of the temporal bone. Anatomical locations for these muscles were determined using multiple sources, including Borst et al. (2011), Grujičić (2023), Karunaharamoorthy (2023), Sendić (2023), and Shahid (2023).

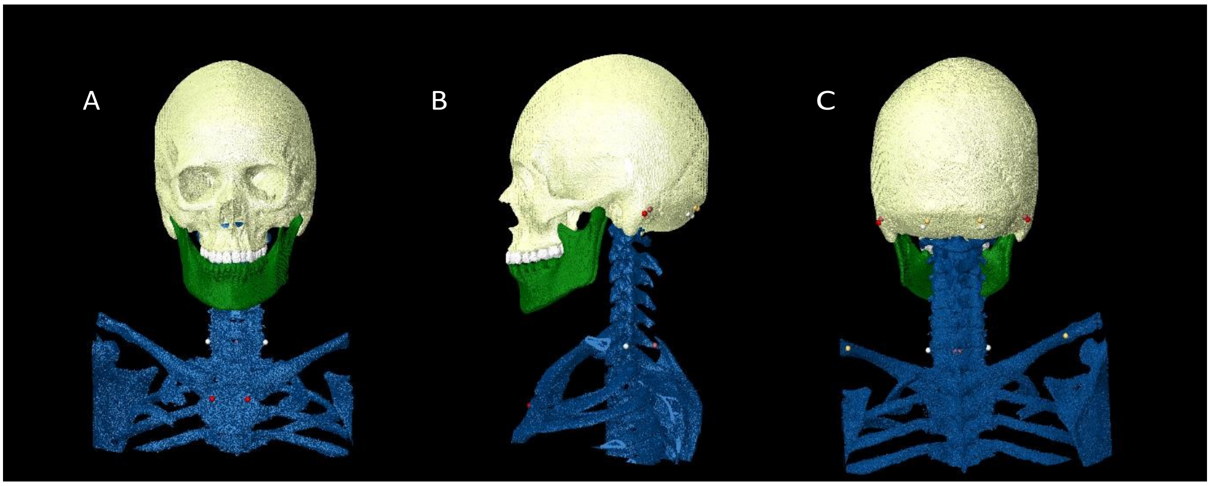

Fig 3.08: Placement of landmarks for the neck extensor muscles used in this study. a) Frontal view of the origins and insertions. b) Lateral view of the origins and insertions. c) Rear view of the origins and insertions.

3.2.5 Finite Element Model Construction

3.2.5.1 Muscle Definition

Upon importing the segmented models into VOX-FE as BMP stacks (.bmp), the first step was to define the muscles of mastication and the selected neck extensor muscles. Using the "node selection" tool, regions of muscle origin and insertion were designated as individual force application sites. The shape and extent of each muscle attachment were guided by a combination of peer reviewed anatomical references and observable morphological features of the specimen (Cunningham, 1914; Vancouver Island University, 2018). For example, the boundaries of the temporalis muscle were reconstructed based on the extent of the temporal fossa and its associated fascia (Elsevier, 2024). Once the muscle origin sites were digitally "painted" following the colour-coding established in Avizo, the previously placed landmarks were used to define the corresponding insertion points. This allowed the directional vectors of the muscle forces to be accurately defined, ensuring that subsequent biomechanical simulations would more closely replicate realistic loading conditions during biting and anterior pulling.

Four neck extensor muscles (sternocleidomastoid, semispinalis capitis, splenius capitis, and trapezius pars descendens) were modelled. These particular muscles were selected based on their important roles in head stabilisation, their direct cranial attachments, and their frequent activation during biting and head-loading behaviours reported in electromyography (EMG) studies (Tecco and Festa., 2010; Hellmann et al., 2012; Giannakopoulos et al., 2013; Im et al., 2015).

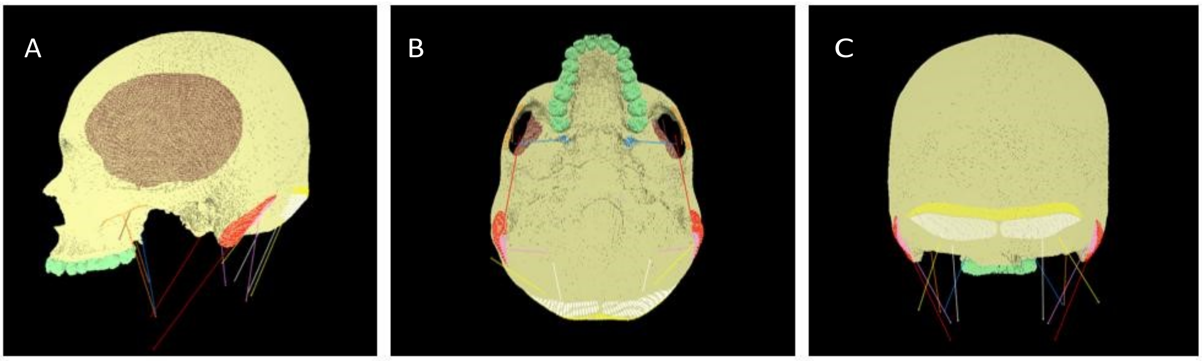

Fig 3.09: VOX-FE model with all necessary muscles included, displaying force directions and end points in a) lateral b) inferior and c) posterior view.

3.2.5.2 Loading and Boundary Conditions

Human cranial bone exhibits complex material behaviour, varying in density, porosity, and mechanical properties depending on age, sex, mineral content, and anatomical location (Falland-Cheung et al., 2017). Given these complexities, and consistent with standard practice in finite element analysis, the cranial bones were modelled as homogeneous isotropic materials (Richmond et al., 2005; Libby et al., 2017). A Young's modulus of 17 GPa was assigned to cranial bone, representative of the lower range of cortical bone stiffness in humans (Szabo & Rimnac, 2022), while the teeth were assigned a modulus of 50 GPa. Both materials were given a Poisson's ratio of 0.3 (Meijer et al., 1993; Richmond et al., 2005;

Gröning et al., 2011; Panagiotopoulou et al., 2017). Although a simplification, this approach allows for direct comparison with previous FE studies while acknowledging known limitations.

3.2.5.3 Calculation of Muscle Forces

Muscle forces for the masticatory muscles were estimated following the protocol described by Toro-Ibacache et al. (2016a). For this, CT slices were aligned to anatomical planes (Frankfurt plane for temporalis measurements; plane parallel to the inferior-posterior margin of the zygomatic bone for masseter and medial pterygoid measurements), and landmarks were placed at standardised anatomical locations (Weijs & Hillen, 1984). Regional thresholding and manual segmentation were used to extract cross-sectional areas (CSA) from three adjacent slices per muscle (1 mm apart), and an average CSA was calculated. Muscle force (F) was then estimated using the equation:

$$F = CSA \times 37\ N/cm^2$$

Where 37 N/cm^2 represents a standard intrinsic masticatory muscle stress value (Toro-Ibacache et al., 2016a).

For neck extensor muscles, CSA measurements could not be reliably obtained from the CT scans. Therefore, published PCSA values from Borst et al (2011) were used to complete the equation. Although these values were derived from an elderly male specimen, no scaling was applied based on the rationale outlined by Östh et al. (2017), who argue that opposing effects of age and sex may cancel out in biomechanical scaling for neck muscles. The intrinsic muscle stress for neck muscles is thought to range between 26.8 – 40N/cm^2, therefore the same value as the masticatory muscle (37 N/cm^2) was used to calculate the muscle force (Brolin et al., 2005; Persad et al., 2024).

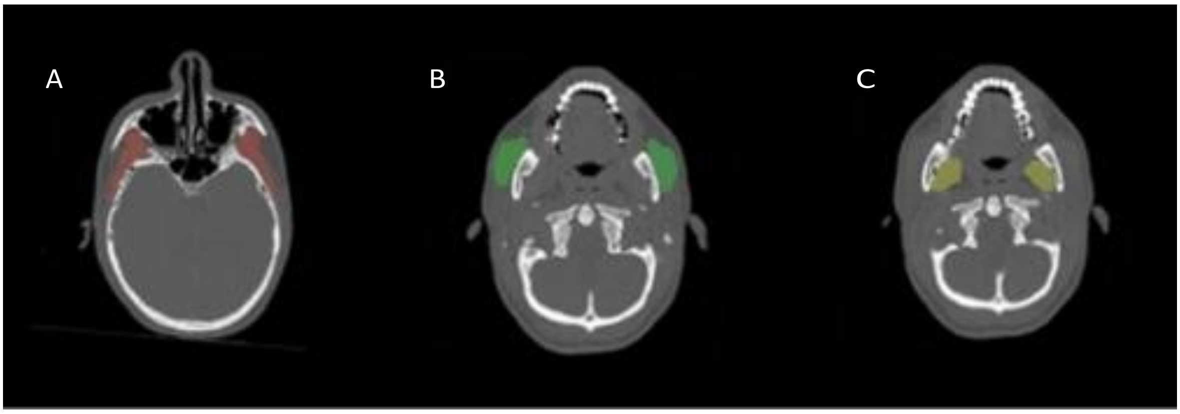

Fig 3.10: Cross-sectional areas of masticatory muscles. a) temporalis b) masseter and c) medial pterygoid.

Table 01: Calculated maximum muscle forces (N) for the masticatory and neck extensor muscles. Masticatory forces calculated from CT scan measurements in Avizo; CT voxel size 0.38 x 0.38 x 0.38; Number of elements: 8,622,751. Neck extensor forces calculated using PCSA values from Borst et al., 2011.

Masticatory (Fmax)			Neck Extensor (Fmax)			
Temporalis	Masseter	Medial Pterygoid	Sternocleidomastoid	Upper Trapezius	Semispinalis Capitis	Splenius Capitis
204.703	214.434	131.535	107.337	130.869	140.896	92.5

3.2.6 Boundary Conditions and Sensitivity Setting

3.2.6.1 Standard Constraint Setup

In the initial model setup, boundary conditions were applied to simulate a vertical incisal bite. For the Incisor constraint, nodes at the midpoint of the maxillary central incisors were constrained in the Y-axis only to simulate stable bite loading. The temporomandibular joint articulation (glenoid fossa) on both the left and right sides of the skull were constrained in the three translational axes (X, Y, and Z), to simulate a static instantaneous scenario (Kupczik et al., 2009; Bright & Rayfield, 2011; Godinho et al., 2017; Stansfield et al., 2018; Brachetta-Aporta & Toro-Ibacache, 2021).

The number of constrained nodes and the precise areas selected were based on standard approaches used in previous studies (e.g., Bright & Rayfield, 2011; Godinho et al., 2017; Stansfield et al., 2018) and were kept consistent initially to allow comparison across sensitivity tests (see Figure 3.11).

3.2.6.2 Sensitivity Variations

To explore the potential impact of constraint definitions on craniofacial strain results, several variations to the standard boundary conditions were created:

1. Anterior Pull Loading: To replicate the type of forces used in daily paramasticatory activities, additional anteriorly directed pulling forces were incorporated alongside the standard vertical bite constraints. Because this form of dual loading (vertical reaction + anterior pull) has not previously been modelled in VOX-FE, it was first necessary to establish a way that this was achievable given the software limitations. Six different combinations of anterior force placements were tested to determine which configuration best produced the desired mechanical effect: a simultaneous vertical bite reaction and anterior loading vector simulating pulling or tugging behaviours (e.g., gripping objects between the teeth while pulling). The anterior force magnitude was standardised to 100 N across these tests for consistency, with future behavioural simulations (Chapter four) potentially applying varying magnitudes based on muscle activation data.

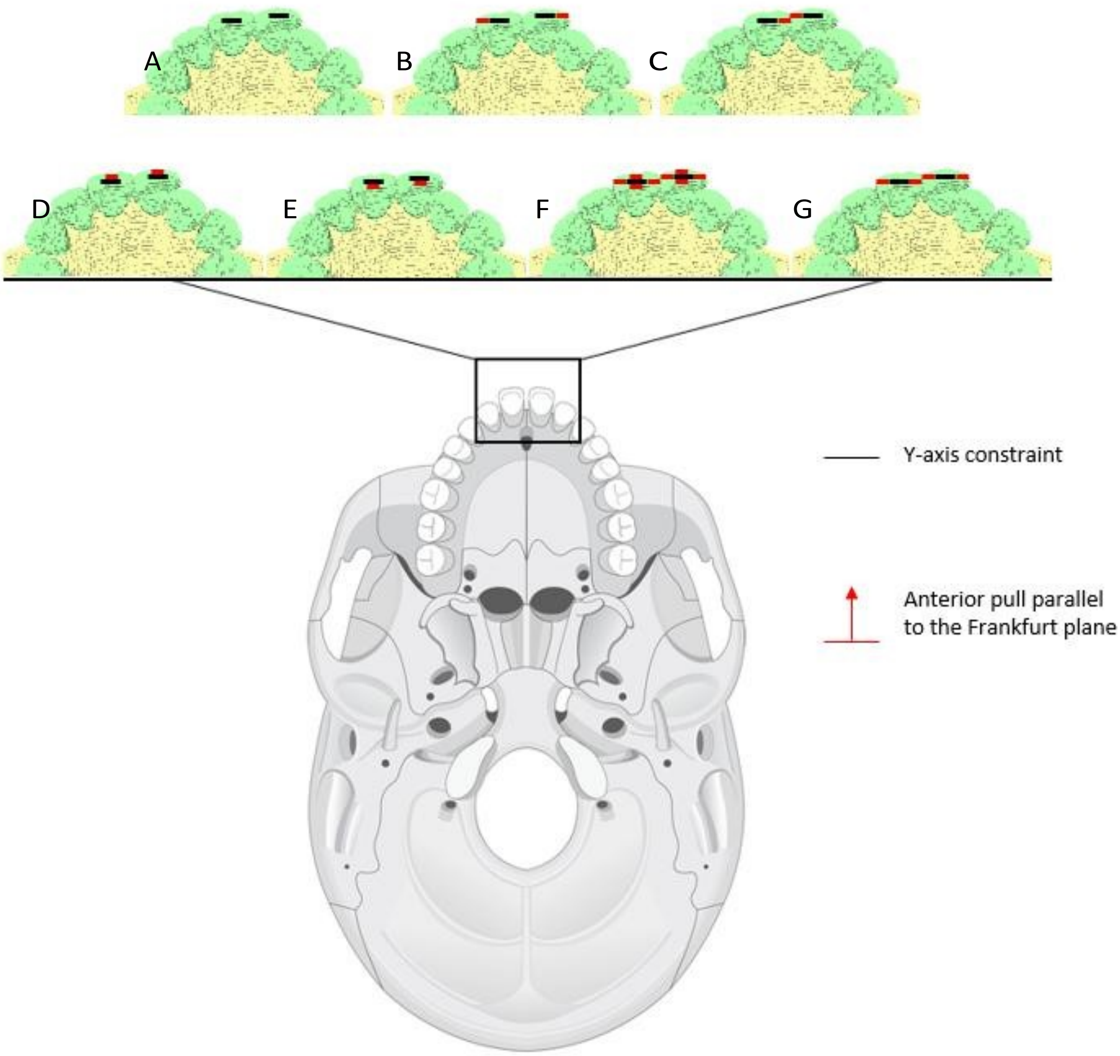

Fig 3.11: Illustration of anterior pull placements in context with the incisor constraint. a) Incisor constraint only b) anterior pull is placed laterally to the incisor constraint c) anterior pull is placed medially to the incisor constraint d) anterior pull is placed anteriorly to the incisor constraint e) anterior pull is placed posteriorly to the incisor constraint f) anterior pull is placed in all four directions of the incisor constraint g) anterior pull is placed laterally and medially to the incisor constraint.

2. TMJ and Occipital Condyle Constraint Variations: (The placement of the TMJ constraint was also systematically varied)

- Standard position: the midpoint of the glenoid fossa (central condylar articulation) (see Figure 3.12-B) was selected (88 nodes in total). The same number of nodes were then selected but in a more anterior position.

- Anterior shift: this was chosen to simulate slight anterior displacement of the mandibular condyle during mouth opening or anterior loading (S. Rathee, 2024).

- Combined (wider area): A larger constraint area encompassing both the mid and anterior portions of the glenoid fossa to account for uncertainty about how load is distributed across the joint surface during different gape angles. 70 nodes were selected on each fossa for this model.

- Occipital condyles: The articular surface of both the left and right occipital condyles (39 nodes each) was constrained in the Y axis only in order to simulate the limited lateral and anteroposterior movement consistent with functional joint mechanics (R. Grujičić, 2019).

This approach allowed testing of how sensitive strain predictions were to small but biomechanically plausible differences in constraint definitions at key functional regions of the cranium.

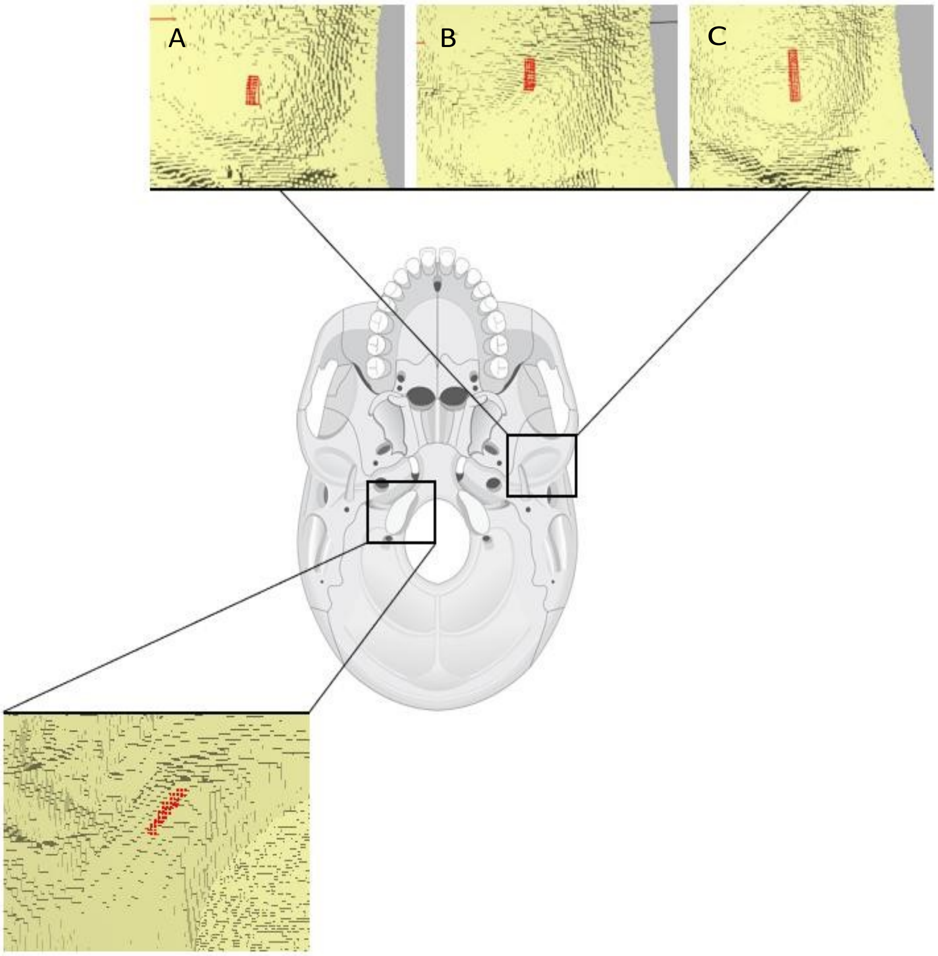

Fig 3.12: Illustration of TMJ and occipital condyle placements on the FE model in VOXFE. All constraints are mirrored on the opposing side on the model. a) Standard position of the left TMJ constraint b) anteriorly shifted placement of the left TMJ constraint c) combined area of the left TMJ constraints d) constraint on the articular surface of the right occipital condyle.

3. Neck Muscle Contribution: The final set of model iterations focused on assessing the influence of neck musculature on craniofacial strain patterns. The four neck extensor muscles were included in isolation and combination in the simulations to investigate their respective and collective contributions to strain distribution. They were modelled individually without anterior pull, and collectively both with and without the application of an anterior pull.

3.2.7 Model Solution and Data Analysis

In total 17 iterations of the female model were created to test the sensitivity of the results to the modelling decisions and ensure the most accurate model is used when going ahead with behavioural testing. In summary, both constraints and loads were varied to test their effects on craniofacial strain patterns. Table 02 below shows the 17 various boundary conditions and loads applied during each simulation.

Table 02: Descriptive table of sensitivity testing model iterations. Anterior pull location is described in relation to the incisor constraint.
Neck muscle abbreviations; SCM = sternocleidomastoid. UT = upper trapezius. SSC = semispinalis capitis. SC = splenius capitis.

Model Name	Constraints				Anterior Pull Location	Neck Extensors			
	TMJ (placement)			Occipital		SCM	UT	SSC	SC
	Central	Anterior	Both						
TMJ1	•								
TMJ2		•							
TMJ3			•						
AP1			•		Lateral				
AP2			•		Medial				
AP3			•		Anterior				
AP4			•		Posterior				
AP5			•		Surrounding				
AP6			•		Lateral & medial				
OC1			•	•					
OC2			•	•	Surrounding				
NM1			•	•		•	•	•	•
NM2			•	•		•			
NM3			•	•			•		
NM4			•	•				•	
NM5			•	•					•
NM6			•	•	Surrounding	•	•	•	•

Once the various female model iterations had been solved using the VOX-FE solver (PARA-BMU) on the Viking High Performance Computing cluster, the resulting nodal displacement files were imported back into VOX-FE for analysis. Strain distributions across the craniofacial skeleton were visualised using global strain maps. Principal strains one (ε_1; maximum principal strain) and three (ε_3; minimum principal strain) were examined within a range of 0–250 με, following protocols outlined in previous studies (Strait et al., 2008; Prado et al., 2016). This strain range was selected to allow for effective visualisation and comparison of strain patterns across models while avoiding oversaturation of the maps.

FEA calculates the strain at each node by analysing the displacement field produced under the specified loading conditions. These strain values are visually represented as global strain maps To allow for systematic, quantitative comparisons across different loading conditions and constraint scenarios, especially between models, specific nodes were selected as strain extraction points. These locations were chosen as they correspond to anatomical landmarks known to experience strain during masticatory loading, based on previous FEA and experimental studies (Smith et al., 2015; Ledogar et al., 2016; Crabtree, 2023).

Strain values at these points were extracted to quantify both localised and regional strain variation between model iterations. The anatomical locations of the extraction points are listed in Table 03 and highlighted in figure 3.13 below.

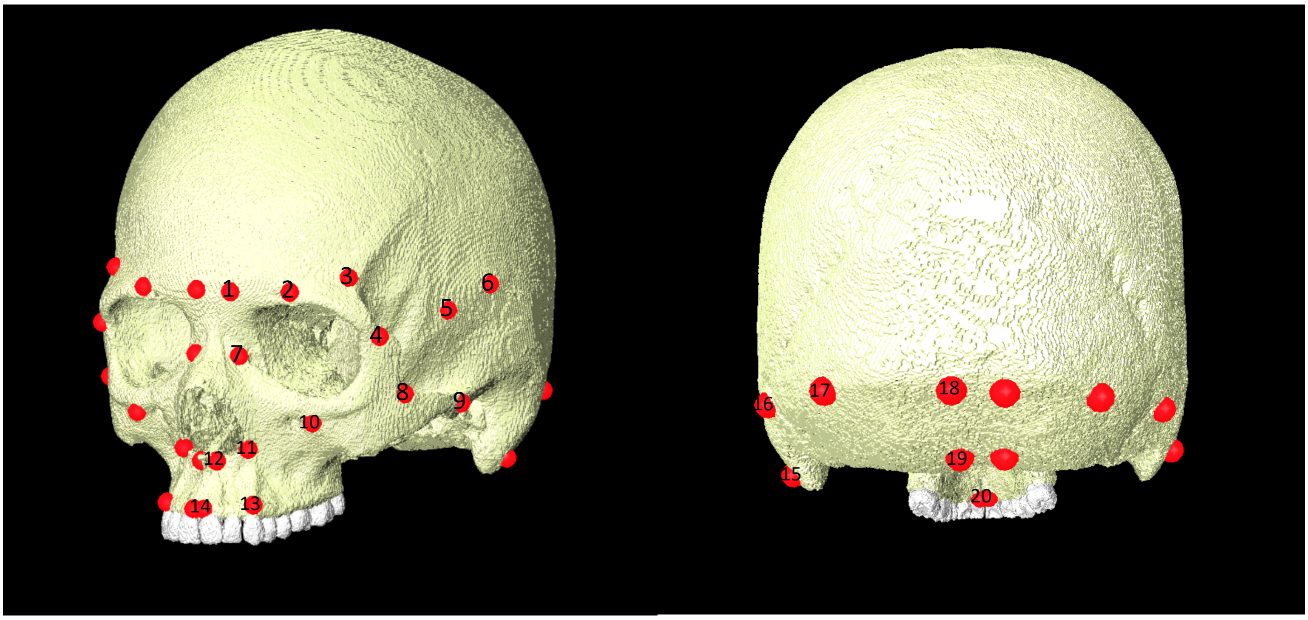

Figure 3.13: Anterior and posterior views of extraction points used for strain extraction on the female model.

Table 03: Anatomical description of landmark placements on both the left and the right side of the skull.

Landmark number	Anatomical Feature	Description
1	Glabella	Lateral to metopic suture
2	Superciliary arch	Lateral to midpoint
3	Temporal corner	Adjacent to temporal line
4	Zygomaticofrontal suture	Midpoint of the suture
5	Temporal bone	Midpoint of anterior portion of squama
6	Temporal bone	Midpoint of posterior portion of squama
7	Frontal process	Midpoint of maxillary frontal process
8	Zygomatic body	On the angle formed between the temporal and frontal processes
9	Temporal process	Zygomatic process articulation
10	Infraorbital foramen	Lateral to foramen
11	Nasal margin	Lateroinferior border
12	Anterior nasal spine	Either side of the spine
13	Intermaxillary suture	Anteroinferior on the left and right side
14	Alveolar process	Superior to canine
15	Mastoid process	Lateroinferior portion of SCM insertion
16	Occipitomastoid-lambdoid	Point at which both sutures meet
17	Superior nuchal line	Lateral point
18	Inferior nuchal line	Lateral to medial point
19	Superior nuchal line	Lateral to medial point
20	Intermaxillary suture	Posteroinferior on the left and right side

3.3 Results

This section presents the results of the sensitivity analyses designed to test the key hypotheses outlined in Section 3.2. For clarity, the results are structured according to each hypothesis tested. Where relevant, qualitative descriptions of strain distributions are supported by extracted strain magnitudes at specific craniofacial landmarks. Global strain patterns are also compared visually across model iterations to assess the impact of loading and constraint variations.

3.3.1 Hypothesis One: Effects of Temporomandibular Joint Constraint Placement

Hypothesis 1 predicted that the placement of the TMJ constraint would affect strain magnitudes and distributions, during biting simulations particularly near the midface and cranial base.

To test this, models were generated with three different TMJ constraint placements: Standard, anteriorly shifted, and a combination of both (see Figure 3.12). Global and local strain patterns were then compared across these models, focusing particularly on landmarks local to the constraint, and in the midface (landmarks 5, 9 & 11; Table 03). The strain maps revealed no change in global strain patterns, with only small, localised differences at the site of the TMJ constraint and medial pterygoid attachments (Figure 3.14).

Results show that altering the placement of the TMJ constraint had a negligible effect on strain outcomes (see Table 04). Differences in principal strains (ε_1 and ε_3) at the key landmarks were minimal, with the overall standard deviation between models ranging from 71.224 and 63.193 microstrain (με). Similarly, predicted bite forces varied by only 6N between iterations.

Table 04: Standard deviation of internal and external strain across three TMJ placement models at specific landmarks.

	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Landmark 5 (Temporal Bone)	16.62	10.41
Landmark 9 (Temporal Process)	31.16	16.94
Landmark 11 (Nasal Margin)	11.63	8.45

These findings suggest that within the range tested, TMJ constraint placement has only a minor, highly localised impact on strain patterns at the glenoid fossa, with negligible effects propagating to the surrounding craniofacial skeleton.

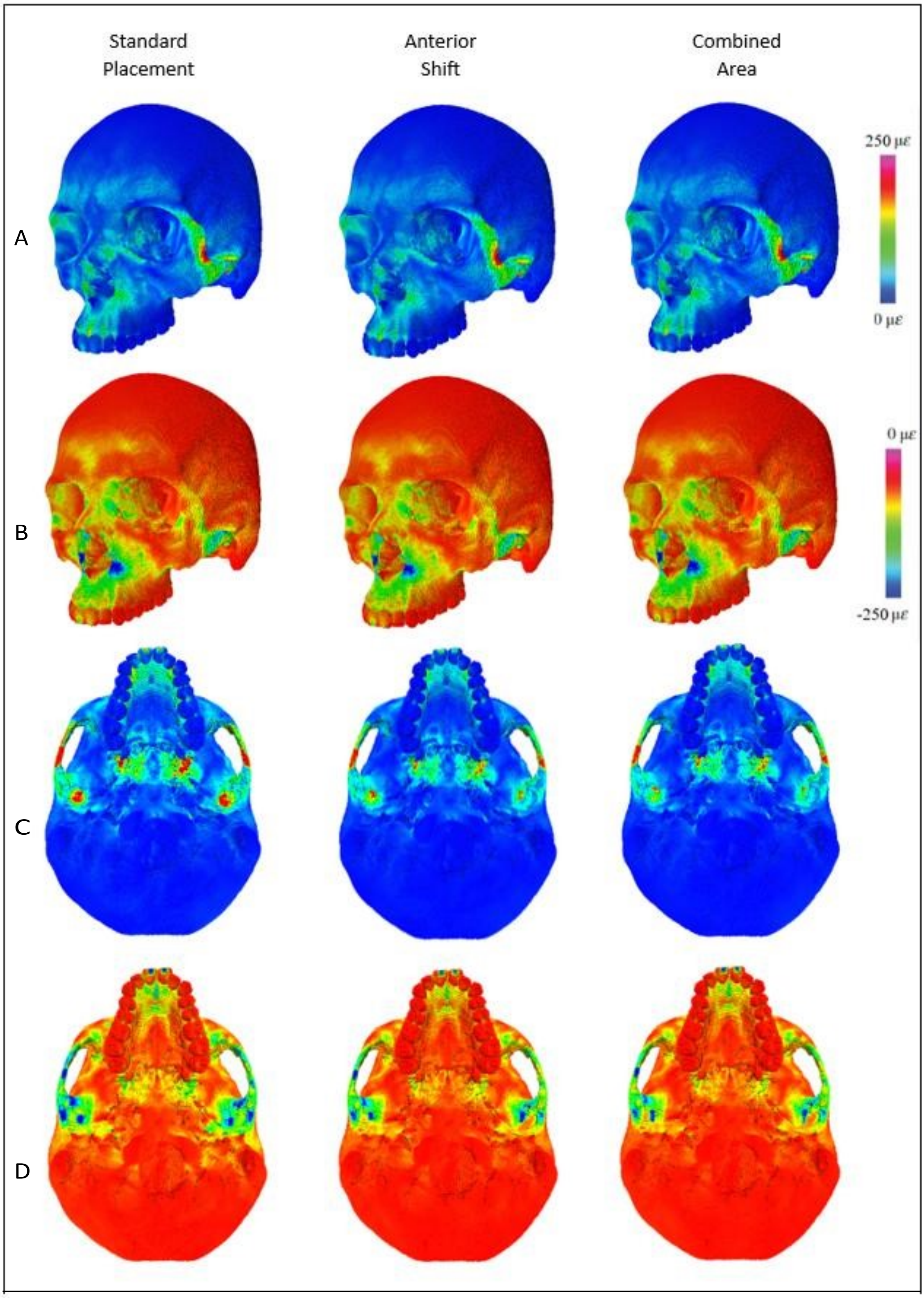

Figure 3.14: Global strain maps produced in FEA for TMJ placement iterations of the female model. a) Principal strain 1 (ε_1) results for facial and temporal region b) Principal strain 3 (ε_3) results for facial and temporal region c) Principal strain 1 (ε_1) results local to TMJ articulation d) Principal strain 3 (ε_3) results local to TMJ articulation.

3.3.2 Hypothesis Two: Impact of Location of Anterior Pull at the Incisors

Hypothesis 2 predicted that the location of anterior pull forces applied to the incisors will significantly impact craniofacial strain outcomes.

To test this, models were generated with six different anterior pull placements relative to the incisor constraints (see Figure 3.11): lateral, medial, anterior, posterior, surrounding, and a combined lateral and medial placement.

Global and local strain patterns were then compared across these models, focusing particularly on landmarks local to the pulling force, and in the midface (landmarks 1, 12, 13 & 20; Table 03). The strain maps revealed no change in global or local strain patterns for the majority of the pull force placements, with the exception of a slight reduction in principal strain 3 at the glabella when the anterior pull is placed laterally to the incisor constraint, as well as localised reduction at the intermaxillary suture for both principal strains 1 and 3 (Figure 3.15).

Table 05: Standard deviation of internal and external strain across six anterior pull placement models at specific landmarks.

	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Landmark 1 (Glabella)	6.77	14.29
Landmark 12 (Anterior Nasal Spine)	9.85	40.79
Landmark 13 (Intermaxillary Suture – Anterior)	23.02	18.16
Landmark 20 (Intermaxillary Suture – Posterior)	13.57	23.27

Results show that altering the placement of the anterior pull force had a negligible effect on strain outcomes. Differences in principal strains (ε_1 and ε_3) at the key landmarks were minimal, with standard deviation between models ranging from 6.77 and 40.79 microstrain (με). Similarly, predicted bite forces varied by only 1N between iterations.

These findings suggest that within the range tested, anterior pull force placement has only a minor impact on incisal strain patterns, with negligible effects propagating to the surrounding craniofacial skeleton.

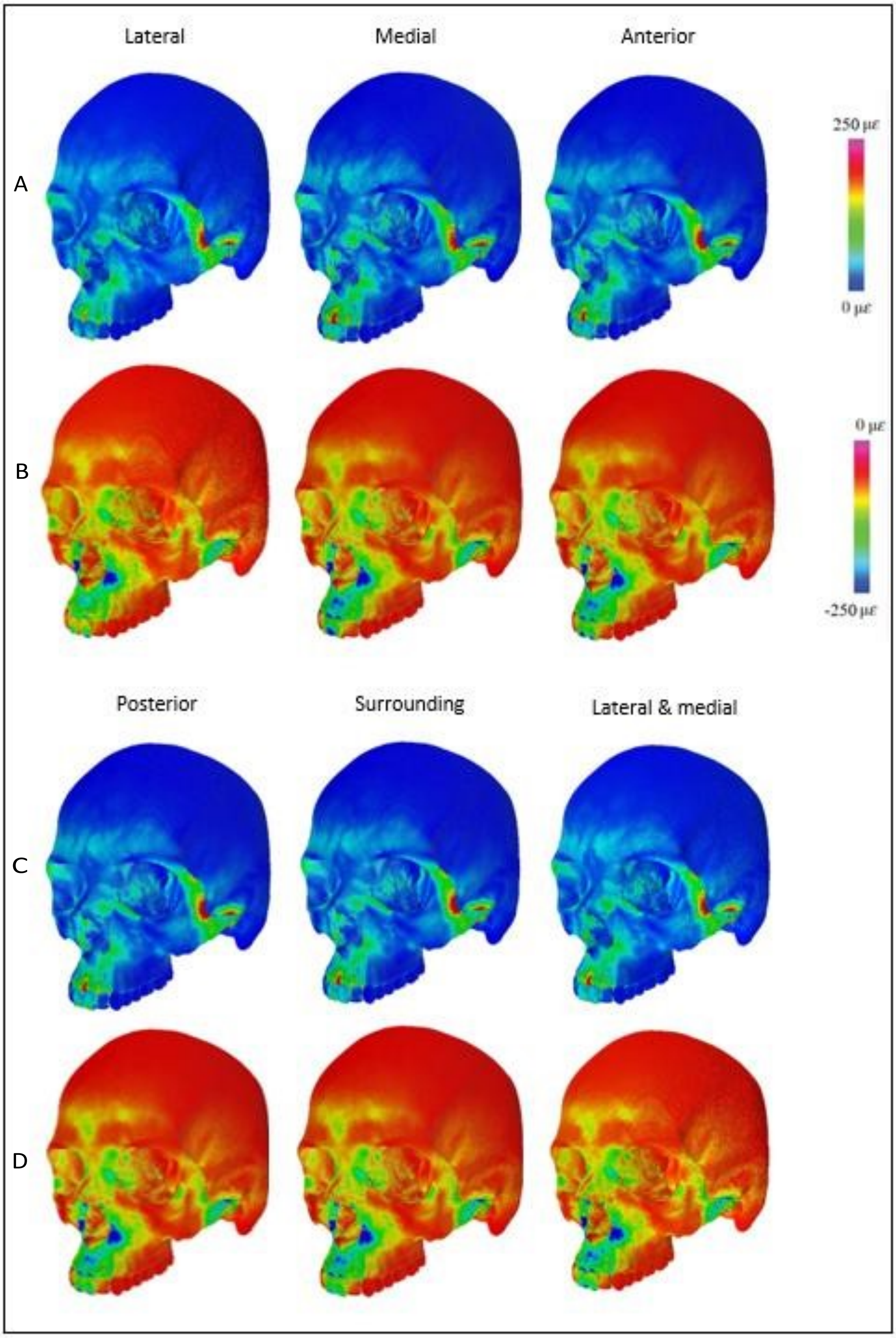

Figure 3.15: Global strain maps produced in FEA for anterior pull force placement iterations of the female model. a) Principal strain 1 (ε_1) results for lateral, medial, and anterior iterations b) Principal strain 3 (ε_3) results for lateral, medial, and anterior iterations c) Principal strain 1 (ε_1) results for posterior, surrounding, and lateral and medial iterations d) Principal strain 3 (ε_3) results for posterior, surrounding, and lateral and medial iterations.

3.3.3 Hypothesis Three: Effect of Occipital Constraint Inclusion

Hypothesis 3 predicted that the inclusion of occipital condyle constraints will primarily influence strain distributions at the cranial base but have minimal effects on midfacial strain during anterior loading.

To test this, models were generated with the inclusion of occipital condyle constraints (see Figure 3.12) both with and without and anterior pulling force. Global and local strain patterns were then compared across these models, focusing particularly on landmarks local to the constraint, and in the midface (landmarks 5, 11, 13 & 18; Table 03). The strain maps revealed no change in global strain patterns, with only minor localised differences at the site of the occipital condyle constraint (Figure 3.16).

Table 06: Standard deviation of internal and external strain across models with and without occipital constraints at specific landmarks.

	Without Anterior Pull		**With Anterior Pull**	
	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Landmark 5 (Temporal Bone)	11.43	1.32	19.91	10.37
Landmark 11 (Nasal Margin)	11.92	5.77	13.01	9.48
Landmark 13 (Intermaxillary Suture - Anterior)	21.04	8.19	38.96	21.49
Landmark 18 (Inferior Nuchal Line)	0.56	0.33	0.96	1.08

Results show that including occipital condyle constraints had a negligible effect on strain outcomes. Differences in principal strains (ε_1 and ε_3) at the key landmarks were minimal, with standard deviation between models ranging from 0.33 and 21.04 microstrain (με) when comparing the occipital condyle model with no anterior pull to the standard model. Standard deviation of between 0.96 and 38.96 microstrain (με) was seen when comparing the occipital condyle model with an anterior pull to the same anterior pull model without the occipital condyle. Similarly, predicted bite forces varied by only 7 and 9N between the occipital condyle iterations and the comparable previous models.

These findings suggest that the inclusion of occipital constraints has only a minor, highly localised impact on occipital condyle strain patterns, with negligible effects propagating to the surrounding craniofacial skeleton.

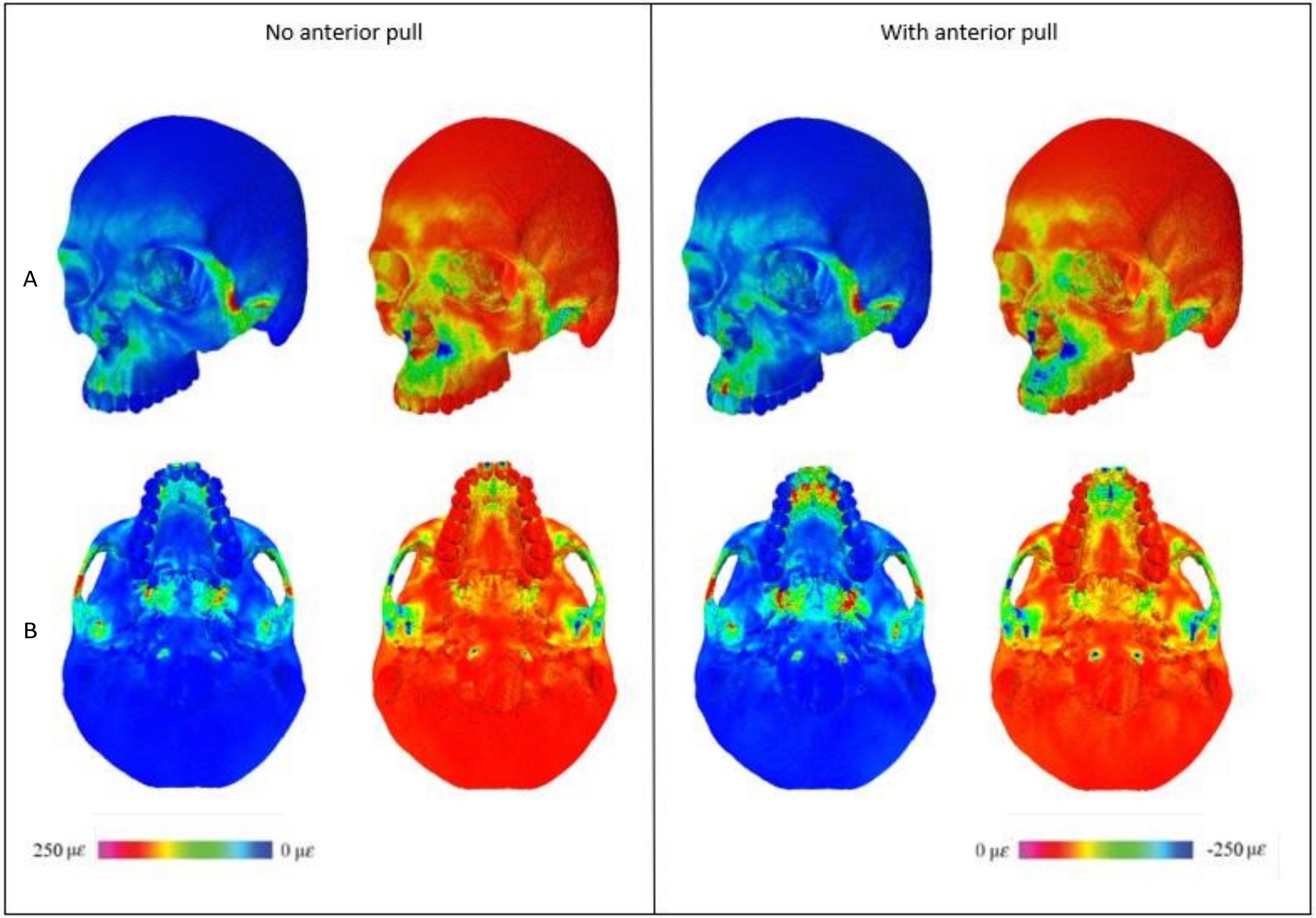

Figure 3.16: Global strain maps produced in FEA for inclusion of occipital constraint iterations of the female model. a) Principal strain1 (ε_1) and 3 (ε_3) results of the facial and temporal regions for both iterations with and without an anterior pulling force b) Principal strain 1(ε_1) and 3 (ε_3) results of cranial base for both iterations with and without an anterior pulling force.

3.3.4 Hypothesis Four: Impact of the Inclusion of Neck Muscles

Hypothesis 4 predicted that the incorporation of neck extensor muscle forces will have a more global effect on craniofacial strain patterns, potentially altering both facial and cranial vault biomechanics, especially during anterior loading scenarios

To test this, models were generated with neck muscles included as a collective, both with and without and anterior pulling force, and also individually. Global strain maps of the models incorporating all of the tested neck muscles displayed changes across the entire craniofacial region both with and without an anterior pull (figure 3.17). The global strain maps of individual neck muscles (figures 3.18 & 3.19) also demonstrate these changes in craniofacial strain patterns, particularly at the brow ridge, nasoalveolar, and temporal regions, as well as localised differences at the individual muscle attachment sites.

Although strain appears to increase across the skull in general when neck muscles were added, there were three areas of change that are key to interpreting the results in a wider research context:

Firstly, the zygoma is an important structure that connects the midfacial region to the neurocranium in order to assist with dissipating strain during biting (Yu & Wang, 2023). Therefore, it is crucial that FE models accurately depict the strain in this region to identify the efficiency of force dispersal during biting, whether in a medical context or for comparing hominin adaptations. As the strain maps show, the addition of neck muscles has an effect on both the internal and external strain in this region which suggests there may be issues with the accuracy of previously published models, particularly comparative hominin models where zygoma vary significantly in presentation.

The second region of focus is the temporal region. As the origin for the temporalis muscle and the site of dissipated strain from the midface and the TMJ, it is important that changes in strain are accurately portrayed in order to assess the efficiency of the skull at handling the internal and external forces from biting. The resultant strain maps in this study show change in this region when the model is loaded with neck muscles, which again suggests more research into the accuracy of loading scenarios is needed.

The third key region of strain to assess is the nuchal region. Changes in strain here are linked primarily to head stabilisation, with species known to have powerful bites often displaying a reinforced nuchal region. It is also attributed to force transmission and so the increase in internal and external strain shown on the strain maps may also indicate a variance in dispersal of strain compared to previously published models which suggests validation of these models is necessary in order to confirm that these models are loaded correctly and producing accurate strain patterns.

Table 07: Standard deviation of internal and external strain across models with and without neck muscles.

	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Without Anterior Pull	75.47	48.49
With Anterior Pull	71.78	53.15

Results show that including the neck extensors had the biggest effect on strain outcomes of all models. Standard deviation was similar both with and without an anterior pull when comparing new models with neck muscles to those without. Predicted bite forces varied by 92N without an anterior pull and 151N with an anterior pull in comparison to the corresponding models without neck muscles.

These findings suggest that within the capacity tested, inclusion of neck extensor muscles has a global impact on craniofacial strain patterns, with substantial effects on the surrounding craniofacial skeleton.

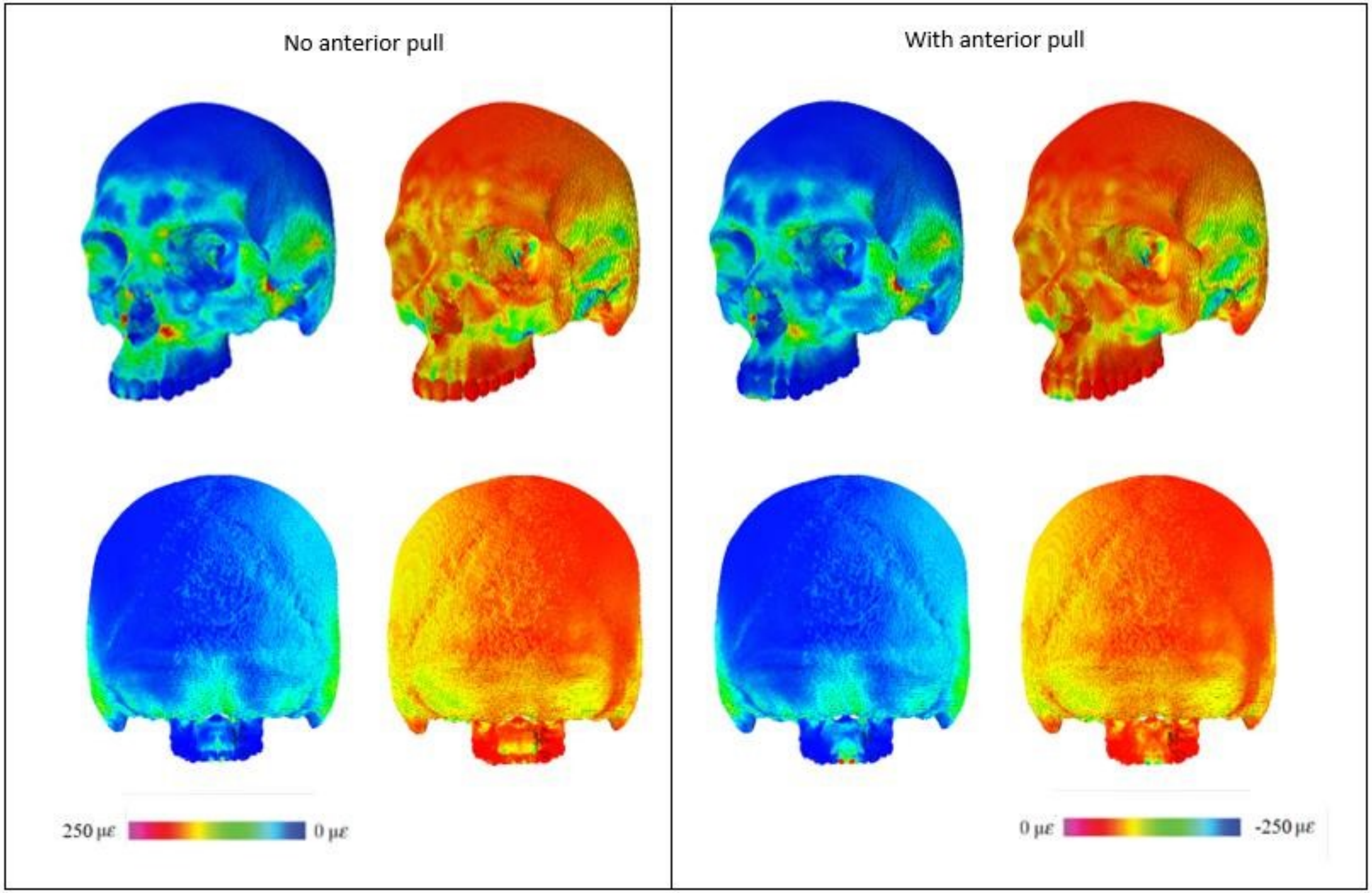

Figure 3.17: Global strain maps produced in FEA for inclusion of neck extensor iterations of the female model. a) Principal strain 1 (ε_1) and 3 (ε_3) results of the facial and temporal regions for both iterations with and without an anterior pulling force b)Principal strain 1 (ε_1) and 3 (ε_3) results of the occipital region for both iterations with and without an anterior pulling force.

As the use of neck muscles is uncommon in this testing scenario, investigating the effects of each individual muscle is important to determine their necessity in future testing. When evaluating the strain maps (see figures 3.18 & 3.19 below), the upper trapezius and semispinalis capitis have the largest visual effect on internal strain, with the exception of the nasoalveolar region. However the effect on external craniofacial strain is fairly consistent for all four neck extensors, again with the exception of the nasoalveolar region, where the external strain appears to increase in the sternocleidomastoid and splenius capitis models, and decrease for the upper trapezius and semispinalis capitis models, in comparison to the standard model with no neck muscles at all.

Table 08: Standard deviation of internal and external strain for six craniofacial regions across individual neck muscle models compared to a model with no neck muscles.

Landmark Group	Sternocleidomastoid		Trapezius pars Descendens		Semispinalis Capitis		Splenius Capitis	
	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Supraorbital Ridge (1, 2, 3)	16.55	9.55	19.50	9.52	20.61	9.65	15.81	9.72
Zygoma (4, 8, 9)	86.44	28.20	88.65	27.97	89.26	27.98	85.17	28.05
Temporal (5, 6)	26.01	11.33	32.07	14.02	34.33	15.00	25.69	11.42
Nasoalveolar (11, 12, 13, 14)	32.88	91.11	28.55	83.16	28.30	75.22	33.93	94.00
Nuchal Region (15, 16, 17, 18, 19)	9.03	3.40	8.07	8.09	9.01	6.24	5.95	2.28
Posterior Maxilla (20)	3.50	15.32	8.64	14.85	12.63	16.30	4.97	15.98

Examining the standard deviation for strain in each region is key for understanding the role each neck muscle plays in strain dispersal. Although there does not seem to be much change in strain visually at the zygoma, the internal strain values show that it is one of the most affected regions for all four neck muscles. This suggests that the zygomatic region is particularly sensitive to loading in the nuchal region, reinforcing the need for further research and model validation.

Conversely, the temporal region appears to show the biggest increase in internal strain when analysing at the strain maps, however when comparing the strain values of the standard model to those of each neck muscle iteration, there is less change than in the zygomatic region for example. This apparent contradiction in the change in strain may be because although a large area of the temporalis displays a change in strain, the intensity of the strain itself is not high.

The nuchal region displays only small changes in strain, localised to the neck muscle attachment sites. This is also seen to be the case when looking at the standard deviation for this region across the five models. The minimal change in this region supports the fact that the primary function of these muscles is head stabilisation, and so bigger changes could be expected to be seen in a model with an anterior pull.

Other areas of interest include the nasoalveolar region, here both the internal and external strain was increased for the sternocleidomastoid and splenius capitis models and reduced for the upper trapezius and semispinalis capitis models. These strain variations are particularly relevant to interpreting the loading scenario, as the nasoalveolar region corresponds to midfacial prognathism — a defining trait in discussions of craniofacial adaptation and masticatory behaviour.

The final region of interest is the brow ridge, where internal strain is consistently more affected than external strain across all four neck muscle models. However, the specific strain patterns vary depending on the extensor muscle added. The sternocleidomastoid and splenius capitis produce a uniform increase in internal strain across the entire brow ridge, while the upper trapezius and semispinalis capitis reduce strain at the glabella and elevate it at the temporal corner relative to the standard model.

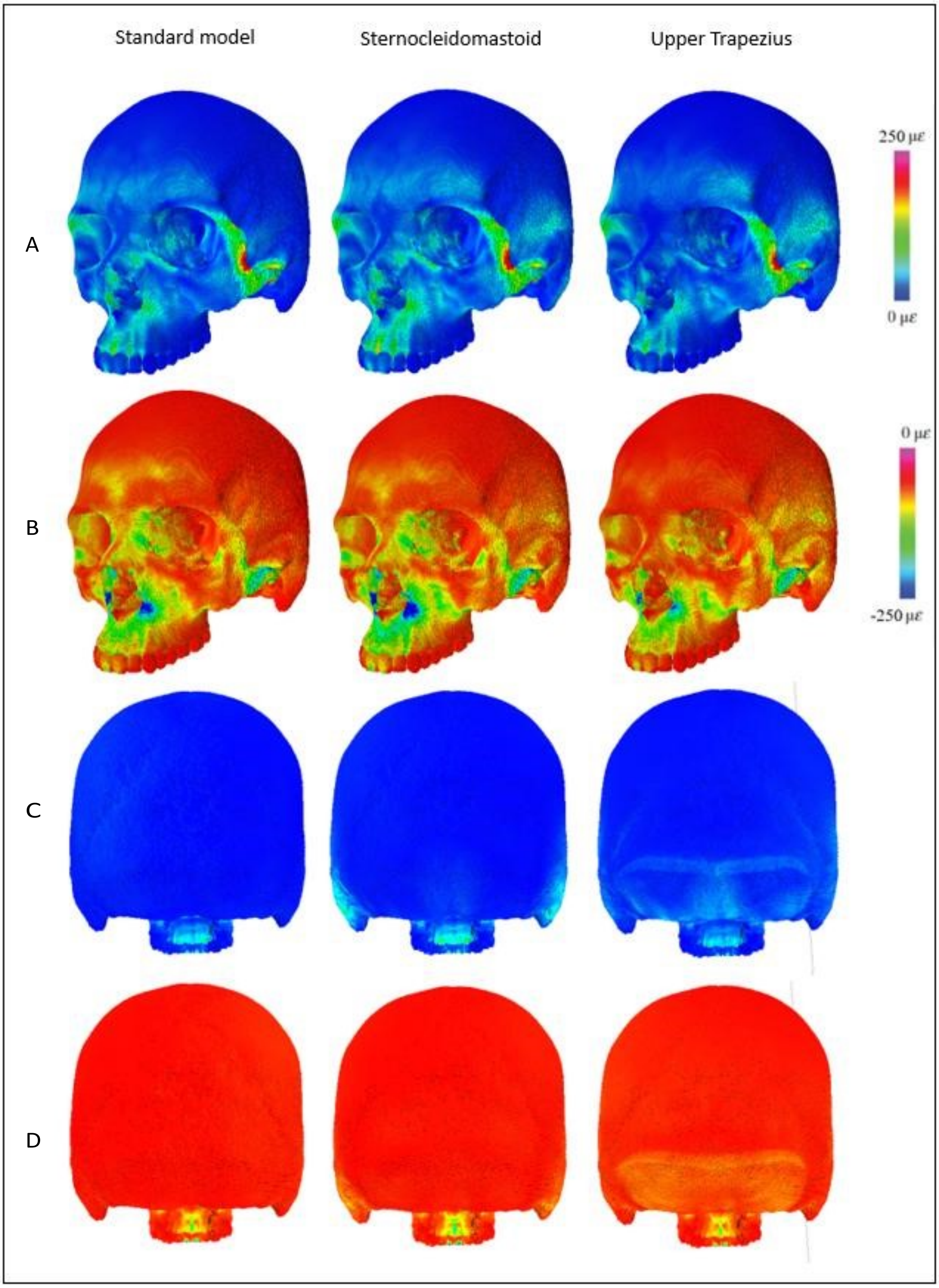

Figure 3.18: Global strain maps produced in FEA for inclusion of sternocleidomastoid, and upper trapezius iterations of the female model, with results of the standard model for reference. a) Principal strain 1 (ε_1) results for facial and temporal region b) Principal strain 3 (ε_3) results for facial and temporal region c) Principal strain 1 (ε_1) results for the occipital region d) Principal strain 3 (ε_3) results for the occipital region.

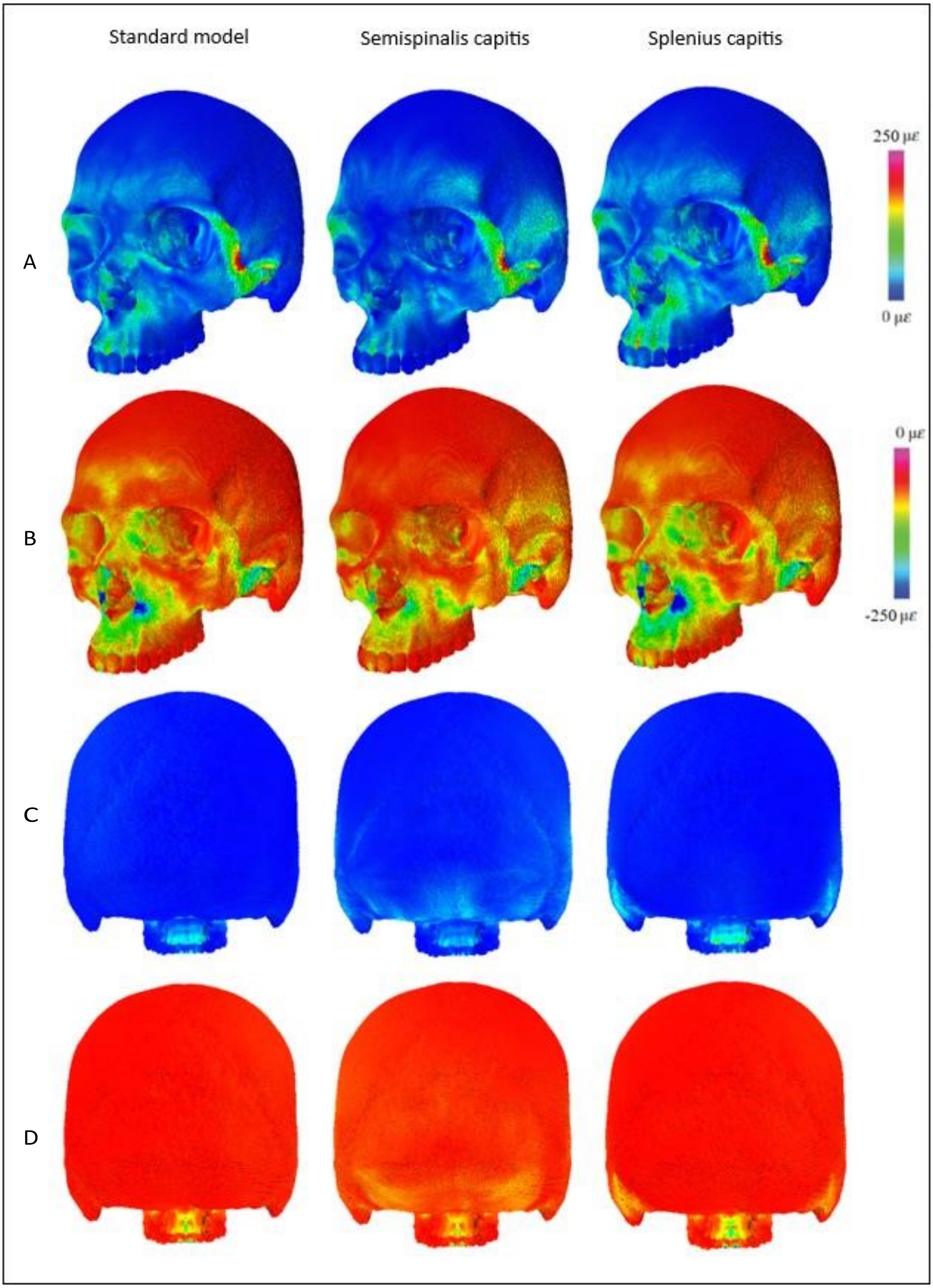

Figure 3.19: Global strain maps produced in FEA for inclusion of semispinalis capitis, and splenius capitis iterations of the female model, with results of the standard model for reference. a) Principal strain 1 (ε_1) results for facial and temporal region b) Principal strain 3 (ε_3) results for facial and temporal region c) Principal strain 1 (ε_1) results for the occipital region d) Principal strain 3 (ε_3) results for the occipital region.

Table 09: Principal strain 1 and 3 values (με) from each landmark for iterations of interest, with standard model values for comparison (see Table 03 and Figure 2.16 for landmark information).

Landmark Number	Standard Model		Combined TMJ Placement		Anterior Pull Surrounding Incisor Constraint		Occipital Constraint		Occipital Constraint with an Anterior Pull		Neck Extensors		Neck Extensors with an Anterior Pull	
	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3
1L	48.896	-18.767	37.450	-13.669	49.401	-18.310	37.300	-13.400	49.500	-18.200	27.300	-46.200	22.600	-31.100
1R	36.169	-46.742	27.235	-35.520	35.992	-46.708	26.600	-34.600	36.200	-46.400	53.900	-24.600	34.900	-15.700
2L	24.281	-12.177	18.782	-9.227	23.806	-12.023	19.100	-9.110	24.800	-11.800	77.600	-18.100	65.900	-14.800
2R	33.938	-16.186	27.101	-13.091	33.658	-15.729	26.600	-12.700	34.400	-16.100	86.600	-36.300	80.600	-31.000
3L	20.533	-11.896	25.239	-12.559	20.268	-11.627	26.800	-13.200	22.200	-12.300	116.000	-44.500	92.400	-36.100
3R	50.328	-26.748	55.493	-27.558	54.813	-27.840	59.000	-28.500	55.700	-28.500	154.000	-66.900	126.000	-53.900
4L	175.513	-61.645	169.249	-59.543	177.839	-62.690	170.000	-59.800	179.000	-63.100	117.000	-36.200	110.000	-34.600
4R	129.804	-42.894	124.031	-41.130	130.283	-42.930	124.000	-41.000	131.000	-43.100	89.500	-35.500	85.000	-34.000
5L	51.152	-32.355	46.953	-28.060	58.787	-34.073	43.100	-25.900	47.300	-30.600	254.000	-100.000	216.000	-87.800
5R	25.515	-30.523	22.676	-24.690	26.666	-30.795	22.000	-25.000	6.730	-8.090	142.000	-63.500	124.000	-58.900
6L	7.596	-7.891	5.678	-6.146	10.106	-9.493	5.340	-6.380	23.100	-29.300	106.000	-94.900	95.200	-86.400
6R	6.505	-5.690	6.514	-3.469	10.518	-4.644	5.370	-4.620	4.710	-6.360	82.100	-62.000	75.000	-55.400
7L	72.966	-65.314	59.148	-53.802	73.547	-66.000	59.200	-53.900	74.700	-66.800	74.200	-78.400	51.200	-52.600
7R	39.341	-83.083	31.201	-65.525	39.254	-83.432	30.800	-64.800	40.200	-85.100	106.000	-53.000	69.300	-35.900
8L	248.753	-102.760	250.963	-103.859	252.356	-104.609	252.000	-105.000	254.000	-105.000	274.000	-108.000	32.700	-67.000
8R	284.385	-101.236	286.869	-102.755	285.910	-101.687	288.000	-103.000	287.000	-102.000	365.000	-137.000	237.000	-93.000
9L	101.063	-44.062	72.835	-40.022	91.950	-42.510	70.500	-39.900	91.600	-42.500	41.500	-105.000	322.000	-120.000
9R	152.882	-78.855	109.335	-61.353	142.006	-74.338	101.000	-58.900	139.000	-73.000	69.700	-136.000	44.300	-78.300
10L	24.788	-22.359	35.166	-29.512	29.440	-24.065	37.200	-29.600	31.100	-24.000	142.000	-151.000	109.000	-120.000
10R	20.824	-20.291	27.350	-31.218	21.495	-21.166	29.000	-33.300	23.800	-23.400	47.300	-90.000	34.700	-67.300
11L	89.475	-266.833	85.443	-251.057	91.145	-271.463	87.200	-256.000	96.100	-285.000	278.000	-94.900	208.000	-70.900
11R	114.029	-274.063	107.927	-258.022	114.331	-275.392	112.000	-267.000	123.000	-296.000	238.000	-99.200	186.000	-78.200
12L	71.534	-95.003	51.085	-76.653	74.958	-94.948	53.700	-79.000	77.100	-103.000	50.500	-50.200	23.800	-20.200
12R	51.214	-64.969	38.502	-53.228	55.576	-68.827	41.600	-57.500	57.300	-73.200	39.400	-34.700	19.000	-14.300
13L	132.284	-145.691	73.483	-73.181	137.258	-149.115	78.000	-77.400	142.000	-156.000	69.400	-66.500	5.280	-16.100
13R	91.128	-109.801	50.926	-56.783	95.272	-113.467	54.300	-60.500	98.100	-118.000	54.700	-47.200	2.740	-8.680
14L	18.200	-70.920	10.314	-41.659	18.504	-71.007	10.900	-43.400	19.100	-74.900	41.000	-10.000	4.680	-1.540
14R	28.986	-54.424	19.086	-31.201	32.265	-57.504	21.100	-33.200	32.600	-58.100	30.200	-19.300	4.390	-8.920

15L	1.952	-0.986	1.660	-0.350	1.884	-0.596	1.860	-0.345	2.190	-0.570	15.100	-15.500	12.400	-12.400
15R	4.535	-3.751	2.418	-2.080	3.336	-2.884	1.510	-1.500	2.420	-2.410	30.200	-12.700	25.600	-10.600
16L	2.353	-3.211	1.225	-1.836	1.819	-2.719	0.851	-1.100	1.670	-1.890	68.200	-32.000	58.400	-26.800
16R	10.207	-16.924	5.333	-8.742	8.510	-13.834	3.720	-6.340	7.610	-13.000	117.000	-58.500	98.000	-47.200
17L	3.233	-7.829	1.370	-4.385	2.080	-5.854	1.040	-3.750	2.470	-6.760	64.100	-30.800	51.900	-25.300
17R	5.372	-5.115	3.284	-2.025	4.976	-2.938	3.440	-1.030	5.630	-2.740	54.200	-49.000	45.200	-39.700
18L	5.220	-4.485	2.094	-1.127	5.172	-1.820	0.867	-0.270	4.320	-3.010	48.900	-49.900	39.500	-39.500
18R	3.160	-2.914	1.469	-0.543	2.598	-0.756	0.657	-0.388	3.460	-3.540	40.000	-27.700	30.800	-20.500
19L	0.965	-1.434	0.300	-0.796	0.817	-0.474	0.269	-0.706	0.734	-0.735	13.800	-23.800	12.000	-20.200
19R	4.567	-3.729	3.417	-2.736	4.683	-3.677	3.460	-2.840	5.270	-4.410	28.100	-36.200	22.200	-28.800
20L	176.645	-94.883	59.825	-46.717	179.645	-99.653	63.800	-49.700	185.000	-101.000	43.800	-68.300	69.400	-30.200
20R	188.496	-135.987	63.219	-72.974	194.405	-143.616	67.400	-78.100	197.000	-146.000	60.800	-60.200	78.800	-25.700

3.4 Discussion

3.4.1 Chapter Overview

This chapter focused on sensitivity testing in order to create a valid finite element model that will be suitable for predicting strain reactions to a variety of anterior dental loading behaviours. Four hypotheses were assessed to achieve this, focusing on the manner in which the model was constrained, the placement of the anterior pull on the incisal ridge, and the inclusion of four neck extensor muscles.

The methods used in this chapter followed published protocols, implementing techniques such as using segmentation to convert computed tomography into three dimensional virtual models. Both masticatory and neck extensor muscle forces were calculated using CSA and PCSA multiplied by intrinsic skeletal muscle strength in order to get estimates accurate enough for sensitivity testing. Numerous model iterations were then tested in a finite element analysis software, collecting bite force and strain information across the crania as a whole, and at specific points of interest.

The results of the sensitivity testing in this chapter will be discussed in more detail with literary context in the subsequent sections.

3.4.2 Temporomandibular Joint Constraint

During mastication, the mandibular condyle undergoes anterior-posterior translational movement within the glenoid fossa (Ingawalé & Goswami, 2009), a dynamic behaviour that cannot be fully replicated in static FE models. To address this limitation, variations in temporomandibular joint (TMJ) constraint placement were tested to assess their effects on cranial strain patterns and bite force predictions.

Results indicated that TMJ constraint position had only a minor influence on overall cranial strain but did affect localised areas adjacent to the joint. Given the uncertainty surrounding jaw joint position during biting and based on comparisons between the two extreme constraint placements and the centralised model, a centrally positioned constraint spanning both the anterior and posterior aspects of the glenoid fossa was selected. This configuration was deemed the most biomechanically appropriate approximation for static bite simulations in light of these uncertainties.

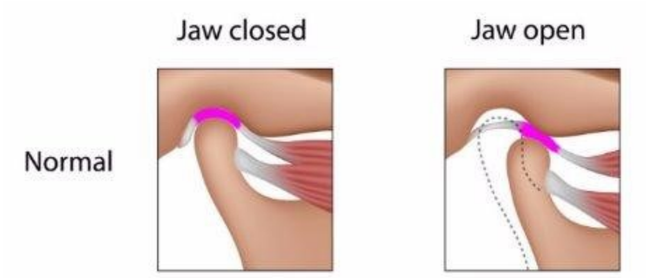

Figure 3.20: Normal movement of the condylar process during biting movement. (TMJ Center, 2025).

3.4.3 Anterior Pull and Incisor Constraint Configuration

As well as changes to the TMJ when performing dental loading behaviours, variations in how the masticatory system is loaded often includes the "tugging" movement of a material clamped at the incisors. This behaviour has not been replicated on human FE models in the literature (Ibacache et al., 2016; Godinho et al., 2017; Ledogar et al., 2017; Wroe et al., 2018). Due to this, sensitivity testing was required to assess the effects of the placement of the pulling force on cranial strain patterns and bite force.

Results indicated that the location of the pulling force on the incisal ridge has a negligible effect on global strains, and a minor effect on incisal strain. When comparing these results to those of the standard model, all present with a small increase in alveolar and incisor strain. As there was negligible difference between the strains of each anterior pull iteration, the configuration of surrounding the incisor constraint was considered the most appropriate for use moving forward. This setup, which distributes force more broadly across the occlusal surface, more accurately reflects *in vivo* loading conditions.

3.4.4 Occipital Condyle Constraint

When modelling an anterior pulling force, it is important to recognise that *in vivo*, the skull would be stabilised by the vertebral column, and so it was deemed necessary to test the effects of including occipital condyle constraints in this study. Due to the fact that the occipital condyles are not constrained in published human models, sensitivity testing was required to evaluate its effects on craniofacial strains both with and without an anterior pulling force present.

This methodological addition represents a novel attempt to approximate physiological boundary conditions more closely, with potential implications for improving the clinical relevance of FE simulations. The results revealed that while condylar constraints had a negligible effect on global strain distribution, they did produce a localised increase in strain at the site of constraint. Importantly, concerns regarding over-constraining the model were mitigated by the consistency of cranial strain patterns and bite force outputs relative to unconstrained models. These findings suggest that the inclusion of occipital stabilisation may improve anatomical realism without compromising model integrity—an important consideration for clinical applications such as surgical planning, prosthetic design, and rehabilitation strategies.

3.4.5 Inclusion of Neck Extensors

Head stabilisation during anterior biting and pulling behaviours is supported by neck extensor muscles, as well as skeletal structures (the spinal column). In clinical and functional contexts—such as mastication, bruxism, or therapeutic jaw exercises—these muscles play a critical role in maintaining cranial stability (Hellmann et al., 2012). However, most finite element (FE) models of craniofacial loading omit neck musculature, particularly in paleoanthropological studies (Ledogar et al., 2013; Godinho et al., 2018; Wroe et al., 2018), limiting their translational relevance to human biomechanics.

To address this issue, sensitivity testing was conducted to evaluate the biomechanical contributions of individual neck extensors and their collective influence on craniofacial strain and bite force. Four muscles commonly cited in clinical research as crucial in head and neck stabilisation during biting—sternocleidomastoid, upper trapezius, semispinalis capitis, and splenius capitis—were selected for inclusion (Ciuffolo et al., 2005; Hellmann et al., 2012; Häggman-Henrikson et al., 2013; Im et al., 2015; Giannakopoulos et al., 2018).

Among these, the sternocleidomastoid produced the greatest effect on global strain patterns, consistent with its known co-activation with the masseter during biting (Giannakopoulos et al., 2013; Fassicollo et al., 2021) and its bilateral role in neck extension and head stabilisation (Bordoni et al., 2022). The splenius capitis showed a similar influence, though with reduced strain in the temporal region and elevated strain at the intermaxillary suture. This aligns with its functional partnership with masticatory muscles (Im et al., 2015) and its clinical association with impaired jaw mechanics when dysfunctional (Naderi et al., 2023; R. Hauser, 2025).

In contrast, the upper trapezius and semispinalis capitis had a more localised impact, with elevated strain near their occipital attachments but minimal effect on global cranial strain. Given their primary roles in shoulder and spinal movement, their limited contribution to craniofacial loading is biomechanically plausible (Häggman-Henrikson et al., 2013).

When all four muscles were included, the model displayed an increase in overall strain magnitude and distribution, highlighting the importance of neck musculature in simulating realistic biting dynamics. Compared to standard models based on established protocols (Bright & Rayfield, 2011b; Fitton et al., 2012; Ibacache et al., 2016; Godinho et al., 2017), these findings suggest that incorporating neck extensors may enhance the anatomical and biomechanical accuracy of FE simulations. Further investigation is vital to refine muscle selection and improve the accuracy of strain predictions in human-based biting models.

3.4.6 Chapter Summary

The form and function of hominin craniofacial skeletons have been investigated through the application of finite element analysis for over two decades, with considerable advances in methodology being made. Masticatory muscle forces and bite locations have been heavily explored with regard to craniofacial strain patterns (Ross et al., 2005; Bright & Rayfield, 2011b; Panagiotopoulou et al., 2011; Fitton et al., 2012; Godinho et al., 2017).

Despite the robustness of these models, many have used simplified configurations that omit fundamental anatomical features such as neck musculature and often simulate a limited number of static bite scenarios, excluding key paramasticatory behaviours such as anterior pulling.

By building on established finite element approaches, this chapter tested the effects of constraint placements, anterior pulling forces, and the inclusion of neck musculature through a series of sensitivity tests designed evaluate whether current modelling approaches are too simplistic.

The results indicate that both anterior pulls and neck musculature influence craniofacial strain, highlighting the need for a more detailed examination of the specific contributions these forces make. For instance, when an anterior pull is applied, what is the magnitude of the loads involved? Likewise, what level of muscle forces do the neck extensors produce to stabilise the head? And simultaneously, what types of forces are generated by the masticatory muscles themselves?

The only way to obtain this information is through *in vivo* data collection, measuring both the external forces generated during pulls and the corresponding activation in the masticatory and neck musculature. Future research should therefore focus on integrating *in vivo* data into finite element models to quantify the mechanical contributions of these forces more accurately and thus allow for a more realistic prediction of craniofacial strain under paramasticatory loading conditions.

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Research Degree Thesis Statement of Authorship

Note that where a paper has multiple authors, the statement of authorship can focus on the key contributing/corresponding authors.

Candidate name	Lauren Spencer
Department	Archaeology
Thesis title	Simulation of Anterior Biting Behaviours: Surface EMG and Strain Mapping of Craniofacial Responses

Title of the work (paper/chapter)	Investigating Craniofacial Strain Patterns in the Context of Realistic Anterior Dental Loading Behaviours	
Publication status	**Published**	
	Accepted for publication	
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	Unpublished and unsubmitted	**X**
Citation details (if applicable)		

Description of the candidate's contribution to the work*	Assisting in the design of the *in vivo* data collection and experimental setup. Leading role in the finite element (FE) model creation, testing, and analysis, and was responsible for the interpretation and writing of the chapter.
Approximate percentage contribution of the candidate to the work (*if possible to describe in this way*)	80%

Signature of the candidate	**Lauren Spencer**
Date (DD/MM/YY)	**03/11/2025**

Co-author contributions

By signing this Statement of Authorship, each co-author agrees that:

(i) the candidate has accurately represented their contribution to the work;

(ii) if required, permission is granted for the candidate to include the work in their thesis (note that this is separate from copyright considerations).

Name of co-author	Laura Fitton
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Description of the co-author's contribution to the work*	Contributed to the conceptual design of the *in vivo* EMG study and coordinated the data collection as part of a broader project. She provided supervisory input on the integration of the experimental data into the FE modelling work and offered guidance and feedback during the analysis and interpretation stages.
Approximate percentage contribution of the co-author to the work (*if possible to describe in this way*)	20%
Signature of the co-author	
Date (DD/MM/YY)	03/11/25

Copy and paste additional co-author panels as needed.

*The description of the candidate and co-authors contribution to the work may be framed in a manner appropriate to the area of research but should always include reference to key elements (e.g. for laboratory-based research this might include formulation of ideas, design of methodology, experimental work, data analysis and presentation, writing). Candidates and co-authors may find it helpful to consider the CRediT (Contributor Roles Taxonomy) approach to recognising individual author contributions.

Chapter 4: Investigating Craniofacial Strain Patterns in the Context of Realistic Anterior Dental Loading Behaviours

Lauren Spencer; Laura Fitton.
Written as for publication with the intention of submission.

Abstract: Humans frequently use their anterior teeth for behaviours other than mastication, many of which impose unique loading conditions on the craniofacial skeleton. Finite element (FE) analysis has long been used to study masticatory loading, yet most models employ oversimplified scenarios (typically static vertical bites) and omit the neck musculature, which is likely active during counter-flexion and stabilising behaviours. This is particularly relevant in paramasticatory tasks involving anterior or oblique pulls on the dentition. Previous research, including Chapter 3 of this thesis, showed that adding anteriorly directed loads and neck musculature can influence predicted craniofacial strain. However, the degree of muscle activation during such behaviours and the magnitude of associated pulling forces remain unknown, limiting the biomechanical realism of current models.

To address this, in vivo muscle activation was recorded using surface electromyography (sEMG) from both masticatory and neck muscles during a range of biting and pulling tasks. These data were then used to apply behaviour-specific muscle forces within the FE model, enabling a more realistic simulation of craniofacial loading during paramasticatory behaviours. The results show that anterior pulling altered strain distribution, particularly in the midfacial, zygomatic, and supraorbital regions, while changes in pull direction further modified strain patterns. Models incorporating neck extensors and in vivo activation data generated bite forces closest to those recorded experimentally, indicating a more realistic loading configuration.

These findings suggest that neck musculature and anteriorly directed forces play a meaningful role in the resulting craniofacial strain patterns. Consequently, studies testing hypotheses about paramasticatory loading should adopt more comprehensive loading configurations that replicate realistic force directions and magnitudes, rather than relying solely on simplified vertical bite models. This should improve the biomechanical relevance of FE analyses and the reliability of interpretations of craniofacial function in both modern humans and fossil hominins.

4.1 Introduction

4.1.1 Dental Loading Behaviours

When comparing paramasticatory tasks from across the fossil record and ethnographic studies, there are many behaviours that are seen to be repeated across both time and geographic location. Many hunter-gatherer groups use their teeth as tools or as a "third hand" which results in shared behaviours due to similar lifestyles. For example, the most common paramasticatory loading behaviour is the use of anterior teeth to clamp plant material during weaving/making cordage. This behaviour has been documented in modern groups such as Native Americans (Schulz, 1977), Neolithic groups such as Breść Kujawski (Lorkiewicz, 2011) and Natufians (Fiorenza et al, 2011), and fossil hominin as far back as Neanderthals (Hardy et al, 2020).

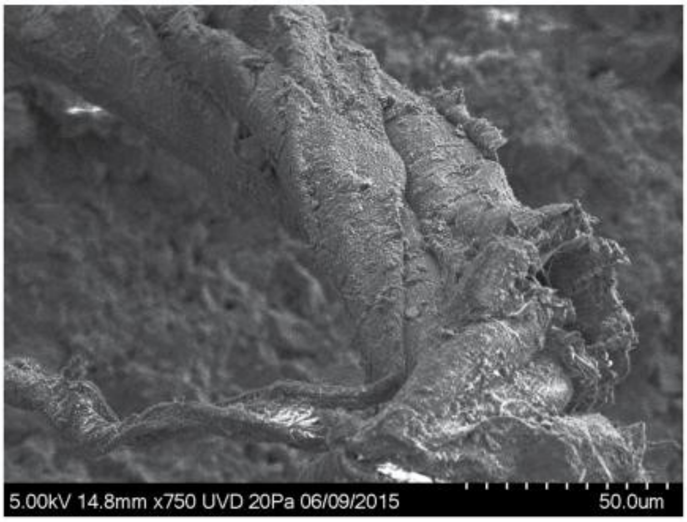

Figure 4.01: SEM photo of multiple fibres presented in a "Z twist" formation on an artefact (Hardy et al, 2020).

Being that it is such a popular behaviour, it stands to reason that it would be a useful one that may be repeated frequently by individuals. As discussed in the first chapter, bone remodelling can occur when lower forces are repeated often. Because of this, behaviours such as cordage weaving that require jaw clamping and an anteriorly directed pulling force on the anterior dentition, should be considered when debating morphological adaptations of the skull.

Ethnographic studies have shown that some modern human hunter-gatherer groups display variations in craniofacial morphology that are thought to be linked to anterior dental loading, such as Inuit groups in Alaska. It is thought that these groups have adapted to their heavy reliance on the use of their teeth as tools with notable changes to their craniofacial characteristics such as; shovelled incisors, a more superoinferiorly shorter ramus, and a coronoid process that is closer to the level of the mandibular condyle (Clement et al, 2012;

Terhune et al, 2018). As such changes can be seen in modern humans, it seems reasonable that changes of this nature could be expected to be found in extinct hunter-gatherer groups too.

Whilst there is a long list of paramasticatory loading behaviours exhibited by hunter-gatherer groups, their movements can mostly be categorised as a “clamp” type bite between their anterior teeth to hold organic material (usually fauna or plant material), a “clamp” bite with an anterior or downward directed pull from either one or both of their hands. There are exceptions to this however, such as flaking rocks using teeth (Molnar, 1972) and placing materials more posteriorly in the mouth to clamp with the molars (Lorkiewicz, 2011).

By simplifying the majority of paramasticatory loading behaviours into these five movements, it makes it a more reasonable expectation to test them all in one study and thus create a well-rounded picture of an individual’s adaptation to the strains caused by anterior dental loading. By testing more than a single incisor bite on future Neanderthal models, together with archaeological evidence, behavioural patterns may be more accurately identified and skeletal adaptations may be found to be linked with them as well.

4.1.2 Surface Electromyography

Electromyography in its essence was created in the 1800’s however it was not until the 1960’s that it was used in a clinical setting (Criswell, 2010), it was around this time that it became a popular research method for scholars as well. By recording the electrical activity produced by skeletal muscles, abnormalities, activation percentage or biomechanics of organic movement can be analysed. Specifically, surface EMG provides a safe, easy, and non-invasive method of recording muscle activation data, but it does have its limitations in comparison to intramuscular electromyography.

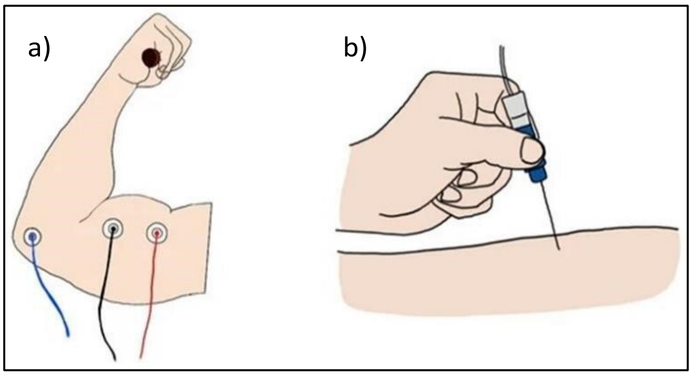

Figure 4.02: Visual representation of the electrodes used in a) surface electromyography and b) intramuscular electromyography (Paunkoska et al, 2024).

Surface electromyography suffers from the systemic limitation of multiple protocols, there are multiple books and videos published on how to place the electrodes on the skin, however no single one has become the practice that all researchers follow, this renders the results from different sources incomparable. For example, any masticatory muscle activities collected in this study could not be directly compared to the results of a paper by Ferrario et al (2004) which measured the temporalis and masseter activations during a maximal jaw clench. This is less of an issue with intramuscular EMG as the needle is placed at various locations in the muscle with repeated data collections to ensure accurate results (Rubin, 2019).

Another limitation of surface EMG is that subcutaneous fat can reduce the signal strength picked up by the electrodes on top of the skin. It is suggested that participants with lower body fat percentages can produce more accurate recordings as the amplitude of the signal is increased. As intramuscular EMG needles generally protrude past the layer of body fat of an individual, this potential reduction in amplitude is avoided (Kuiken et al, 2003).

“Cross talk” is a major limitation faced by surface EMG researchers; this refers to the interference of signals from other muscles being picked up by an electrode. This issue is worse in some areas than others but can prove hard to rectify as the signal from the intended muscle of interest cannot always be isolated (Criswell, 2010). For example, electrodes placed in the dorsal lumber region will likely pick up generic muscle activity in the lower back, rather than the activity of one specific muscle. Although this may not be a problem in some scenarios, it is not ideal for studies requiring EMG data for specific individual muscles. Whilst this phenomenon is not completely erased with intramuscular needles it is reduced thanks to the more precise nature of the electrodes and their locations (Péter et al, 2019).

Despite these limitations, surface electrodes can still be the most appropriate choice of instrument for recording masticatory muscle activity due to their non-invasive nature, as it can be intimidating to potential participants to be requested to perform various tasks with needles inserted into their faces. It is also a much cheaper method, which can be the deciding factor in many studies.

4.1.3 Using EMG Data for Contextual Insight

A 2012 paper by Shaw et al investigated Neanderthals possible skeletal adaptation to spear thrusting. They found that Neanderthals were more likely adapted to scraping tasks, however more interesting than their findings, were their methods. Shaw et al used electromyography (EMG) to monitor chest and shoulder muscle activation for 13 participants during varied activities relating to upper arm function. The data collected from these participants was used to infer causation of Neanderthal humerus adaptations based on proposed forces that would incur bone remodelling.

Outside of genetic research, the concept of using in vivo data for research pertaining to Neanderthals is quite novel, in the case of the spear thrusting paper by Shaw et al the results could simply make suggestions about Neanderthal adaptations as they only tested modern human muscle activation. However, a published thesis by Berthaume (2014) took this method a step further and used the muscle activation data recorded in Shaw's EMG testing to create accurate FE models that enabled them to reject the hypothesis that Neanderthal humeri were adapted to spear thrusting and not spear throwing.

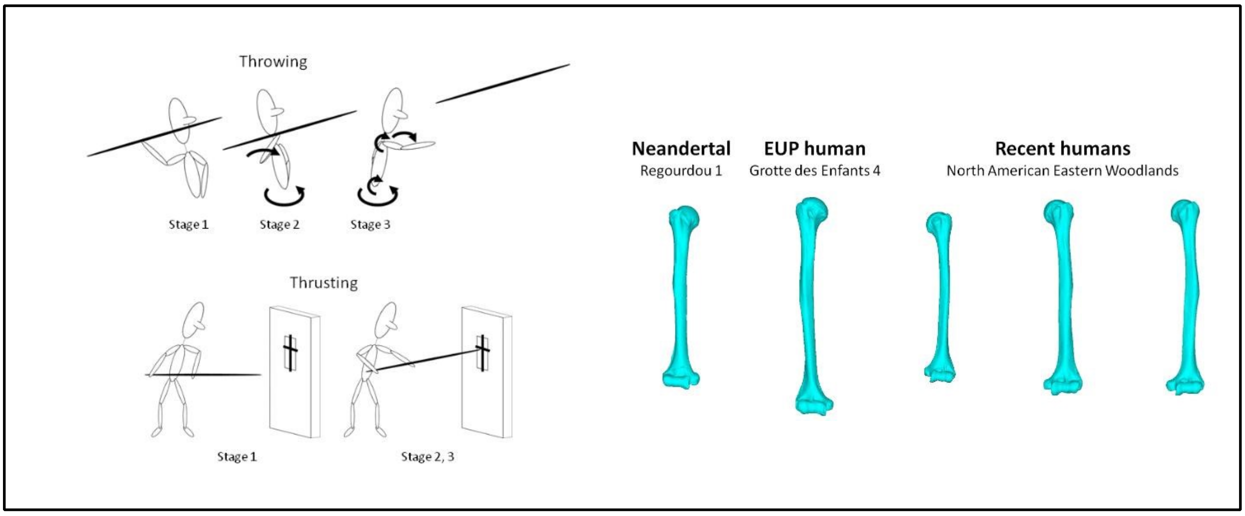

Figure 4.03: Images of the EMG spear throwing and thrusting tasks, and FE models used in Berthaume's 2014 published thesis.

Berthaume's method of using EMG data to improve the accuracy and reliability of his FE models could be used to bring all Neanderthal models closer to realistically representing biomechanical responses to loads. This method of recording EMG data for masticatory and neck muscles during specific movements representative of Neanderthal behaviours could be used in the study of anterior dental loading to help to increase the accuracy of the models and thus the results and conclusions that come from them.

The use of this method as well as testing the inclusion of neck musculature should help to improve the validity of the models and the findings in this chapter. When it comes to producing new research on a well-documented subject such as anterior dental loading, improving the reliability of the results is often the main aim in order to ensure that past conclusions can either be further verified or confidently rejected. Like in Shaw (2012) and Berthaume's (2014) research, behaviour specific muscle activation will help to ensure reliable results are produced when creating new FE models that test the effects of varied paramasticatory loads on craniofacial strains. For these reasons, it was decided that EMG testing would be used in this chapter to further improve the FE models created for the purpose of testing the effects of neck musculature and varied loads on craniofacial stains during anterior dental loading.

4.1.4 EMG and Virtual Modelling

As previously touched upon, the use of EMG data in palaeoanthropology is almost entirely limited to the papers published by Shaw and Berthaume. However, the use of EMG data to create virtual models or for virtual testing is not so novel, research in other areas of biomechanics have used this combination of methods for more than twenty years. Due to its longevity, the use of EMG data in other virtual disciplines should be explored in order to establish its role in paleoanthropological research moving forward.

As far back as 2002, Manal et al used recorded EMG data to control a "virtual arm". This 3D graphical representation of a human arm consisted of the major muscles that interact with the elbow joint and moved in real-time. This study was able to successfully use EMG signals to perform isometric load directed elbow flexion and extension tasks with the virtual arm. As they were able to virtually repeat the movements performed by the participant within 40ms, their participants were able to visualise that they were in control of the arm, and so it stands that using *in vivo* muscle data can help to increase the accuracy of virtual models.

A later paper by de Rugy et al (2012) used EMG recordings for their virtual reconstruction. In their study of wrist movement de Rugy used forces reconstructed from their rectified EMG data multiplied by pulling vectors (designed by a custom algorithm) to perform three virtual and *in vivo* experiments to predict variance in force signals. Their comparison of virtual predicted data and *in vivo* EMG signals showed that their technique worked in multiple contexts which again supports the use of *in vivo* data in virtual modelling – even if in the context of verifying virtual results.

In a more familiar avenue of research Macchi et al (2021) used *in vivo* data to aid their biomechanical investigation of percussive techniques in early stone toolmaking. This is one of very few palaeoanthropology papers to have used EMG in their investigation of the kinematics of fossil hominin since Shaw, but like Shaw they did not take their research further and combine their EMG data with virtual testing in order to add depth and accuracy to their claims. Their analysis of flake production was based on the hypothesis that *Homo* were not the first knappers and that it was likely *Australopithecus* or *Kenyanthropus*. However, they only set out to identify the difference in kinematics of various knapping techniques, without further implications on the origins of stone toolmaking. While the lack of combined *in vivo* and virtual testing sets this paper apart from the theme of this chapter, its use of EMG to recreate the hypothetical movements in a real-life setting further evidences its usefulness and the disciplines slow but purposeful embrace of the method.

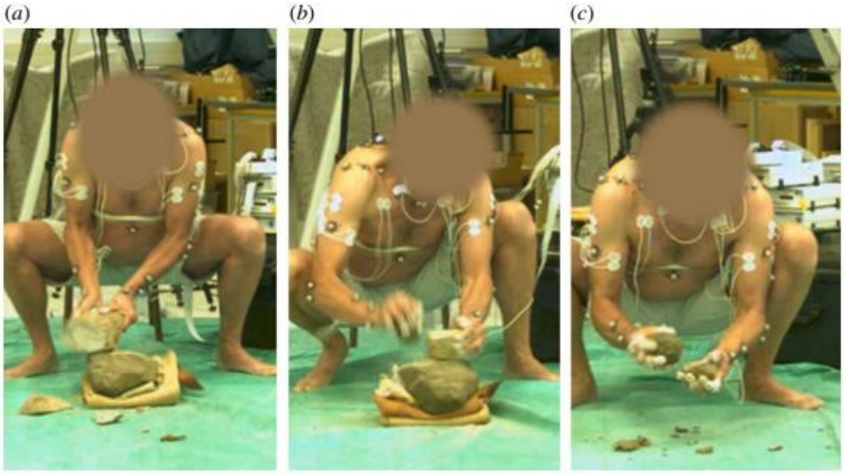

Figure 4.04: Demonstrations of three stone knapping techniques used in Macchi et al's 2021 study (Fig 01, pp 2). A) unipolar flaking on a passive hammer b) bipolar flaking on the anvil c) multidirectional flaking with free hand.

As discussed, the use of EMG data to provide contextual insight and improve the accuracy of virtual testing is minimal in this discipline. However, as it has in the other avenues of research, it is proving to build upon the reliability of the findings being presented on biomechanical theories on fossil hominin. For these reasons' EMG testing will be used in this chapter to further increase the accuracy of the FE models and their findings.

4.1.5 Virtually Investigating Craniofacial Strain Patterns

Based on findings from published research in biomechanical disciplines this chapter will include surface EMG testing in order to collect muscle activation data for both masticatory and neck muscles that will be used to create the muscle forces for the finite element models created in this chapter. These FE models will then be used to test the effects of:

- Using *in vivo* data instead of scaled cadaver values.
- Using neck muscles in biting simulations.
- Varying the biting behaviours recreated by the simulations.

The EMG testing in this chapter will focus on replicating common paramasticatory behaviours. These behaviours will be simplified to five scenarios that that participant will perform three times each in order to lower the effects of anomalous results and produce reliable mean values. These scenarios will include; a maximal voluntary bite at the incisors performed alone, with one- or two-handed anterior pulls, and with one- or two-handed downward pulls.

The FE testing in this chapter will primarily focus on the effects of behavioural changes to the model. Since there is no behavioural variation in current published models, it will be important that these models are loaded correctly to ensure that they are in fact testing what they are designed to. In order to establish that this is the case the use of *in vivo* data and the inclusion of neck muscles will also be separately analysed to ensure that any changes seen in the results of the behavioural models cannot be attributed to these variables instead.

4.2 Aims and Hypotheses

This chapter aims to use surface EMG to quantify neck muscle activity in order to more accurately replicate the effects of varied anterior biting behaviours on craniofacial strain patterns.

Hypotheses:

- Masticatory muscle activation will remain the same but neck muscle activation will increase during anterior dental pulls compared to standard vertical bites.
- Craniofacial strain will increase during a physiologically loaded anterior pull compared to a standard bite.
- Changes in the magnitude of anterior pull force will produce global variations in craniofacial strain distribution, whereas directional changes in the force will result in more localised strain effects.

4.3 Methods

4.3.1 EMG Materials

Surface electromyography (EMG) of the masticatory and neck muscles, alongside bite force data collection, was carried out during a series of bite and pull scenarios. Ethical approval for this study was granted by Hull York Medical School Ethics Committee (ref: 21-

22.56) and the Department of Archaeology, University of York, following the departmental review process. Prior to participation, the participant was provided with a Participant Information Sheet outlining the nature and purpose of the study and signed a Consent Form confirming their voluntary participation. Blank versions of the Participant Information Sheet and Consent Form are included in Appendix (section B). A single healthy adult male in his thirties was recruited as the sole participant. Inclusion criteria specified no history of masticatory or neuromuscular disorders. Although additional recruitment was attempted, particularly of female participants, the requirement for electrode placement over the temporalis muscle (involving partial head shaving) limited participation within the available time frame.

The materials required to perform surface electromyography (sEMG) followed the specifications outlined in Thomas Baird's (unpublished) 2025 protocol. These included the MyoSystem 1400A unit, capable of supporting both surface and fine-wire electrode EMG recordings, along with an active cable configured with eight EMG channels and corresponding preamplified leads. Pre-gelled disposable surface electrodes were used for signal acquisition, and data was recorded using a laptop equipped with MyoResearch XP software. A digital spring gauge was utilised to record and facilitate consistent mechanical pulling forces during testing procedures. A video recording device was employed to capture synchronized visual data. Standard preparation materials included alcohol wipes and adhesive tape. A synthetic leather belt was used by the participant as a biting and pulling implement to simulate the target behaviour and elicit muscle activation. Ideally a 100% leather belt would have been used to replicate behaviours in a realistic manner, as the synthetic material was less resistant to the pulling forces generated in the testing. However, as the research was self-funded, it was not within the budget and time frame to buy one. Finally, the participant was provided with a consent form and an information sheet in accordance with ethical research practices.

Figure 4.05: Image of the equipment necessary for surface EMG testing.

4.3.2 EMG Setup

Surface EMG data were collected using the Noraxon MyoSystem 1400L, connected via an 8-channel active cable to a laptop running MyoResearch software. Pre-gelled surface electrodes were attached bilaterally to the masseter and temporalis muscles, as well as to two neck extensor muscles: sternocleidomastoid, and trapezius pars descendens, based on anatomical landmarks identified by palpation. An electrical reference electrode was placed over the spinous process of the C7 vertebra, a neutral bony site unlikely to be involved in the target muscle activity. Signal gain was set to 54 dB, and filtering parameters were optimised for surface EMG acquisition (bandwidth up to 500 Hz).

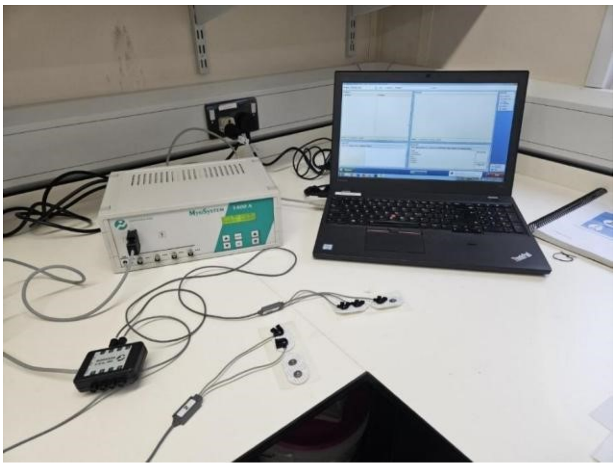

Figure 4.06: Image of the MyoSystem set up in preparation for *in vivo* testing.

Once the equipment was ready for testing, the next stage was participant preparation. Ethical approval was given by the department prior to any testing, and consent was given by the participant via a consent form after having read the experimental protocol, risks, and benefits, etc. The participant was asked to sit on a stool near a black backdrop, adjacent to the myosystem set up.

To prepare the participant for testing, a patch of skin was cleaned with an alcohol wipe and a patch test was performed to ensure there was no reaction to the gel or tape used to adhere the electrode to the skin. Once it was certain there was no reaction, the electrode application sites were then prepped by shaving any areas with too much hair for adhesion, such as the temple, then cleaned and dried with an alcohol wipe and cotton pad.

Once the skin was prepared, the electrodes were placed as per Cram's Introduction to Surface Electromyography (Criswell, 2010). To correctly position the temporal electrode the participant was asked to clench their teeth, the electrode was then placed where a muscle bulge was felt. The same process was followed for the masseter muscle at the corner of the jaw. The medial pterygoid could not be used in surface EMG testing due to its location on the internal side of the mandible.

The electrodes for the upper trapezius were placed at the upper crest of the shoulder, halfway between C7 and the acromion. For the sternocleidomastoid, the electrodes were placed midway between the mastoid process and the sternal notch, slightly behind the centre of the muscle belly. As the semispinalis capitis muscle lies deep to the upper trapezius it is not included in surface EMG studies (Valkeinen et al, 2002) and so for the virtual behavioural testing, activation patterns identified in the literature will be scaled to the male and female models in this study. Finally, the splenius capitis also lies deep to the trapezius, however, rather than include values derived from other research, this muscle will be omitted from the virtual behavioural testing in this chapter based on the findings of Giannakopoulos et al 2013. They found that the EMG activity for splenius capitis was significantly reduced when experiencing anterior forces. Therefore, its inclusion in modelling virtual anterior pulls has been deemed unnecessary for this chapter.

Myoresearch is a biomechanics software from Noraxon that provides real-time data visualisation, and processing tools. It was used in this study to collect the muscle activation data from the surface EMG testing and then to process the data afterwards. In this software continuous tracing was used to record the data, as the signal is shown as a continuous curve, while the sampling frequency selected was 1000Hz which is the standard fir this software. The Myoresearch also has a metronome feature which was used to keep the participants movements uniform and evenly spaced in order to create more easily digestible data.

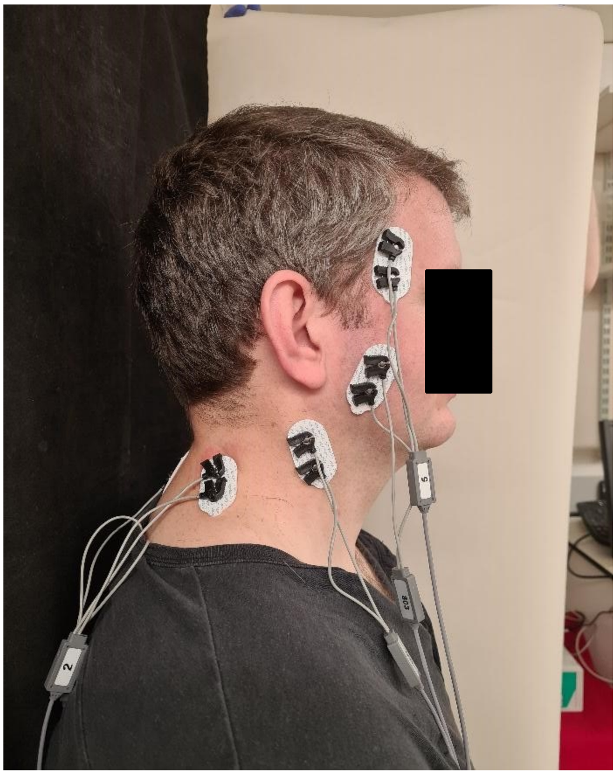

Figure 4.07 Image of electrode placements on participant, from top to bottom; temporalis, masseter, sternocleidomastoid, and upper trapezius.

4.3.3 EMG Data Collection

Once both the equipment and the participant were set up, the first stage of data collection was to record the maximum baselines for each of the muscles being tested. For this study five different movements were used to achieve this based on methods used by Valkeinen et al 2002 and Hellmann et al 2012;

a. Maximum head extension against resistance (straight)

For this test the participant was asked to sit with their back and head resting against a wall, then to push their head back as hard they comfortably could.

b. Maximum head extension against resistance (slight angle to the right)

For this test the participant was asked to sit with their back and head resting against a wall, then to turn their head slightly to the right and then push their head against the wall as hard they comfortably could.

c. Maximum shoulder elevation (right shoulder)

For this test the participant was asked to raise their right shoulder against a force pushing down to keep their shoulder in place. This was done on the right shoulder as the electrodes were all placed on the right side of the participant.

d. Head rotation against resistance

For this test the participant was asked to turn their head to the right against a force pushing their head to keep it in place. This was done on the right side of the head as the electrodes were all placed on the right side of the participant.

e. Maximum jaw clench

For this test the participant was asked to clench tooth on tooth at the molars.

Each of these movements were repeated three times to reduce the impact of anomalous results, and the mean of these results were used where appropriate.

Once this process was completed the maximum bite force needed to be recorded. A load cell was calibrated using the Mecmesin MultiTest-dV 2.5kN and the Emperor Force software. The Mecmesin instrument is a motorised force tester that provides precision-controlled compression and tension testing, and the Emperor Force software allows the design and customisation of such testing. For this test, the participant was asked to bite down as hard as they comfortably could three times on a load cell placed at the incisors with a gape of 15.2mm.

The next stage of testing was to ask the participant to perform the five anterior biting tasks needed for behavioural FE analysis;

1. Maximum incisal bite

An incisal bite is a standard behaviour to be tested for anterior dental loading papers. It is used in this study to represent the generic behaviour of biting anteriorly. So as not to damage the teeth of the participant, a softer material was used for maximum biting. For this test the participant was asked to bite down on a piece of a leather belt placed at their incisors as hard as they comfortably could.

Figure 4.08: Image of participant biting on a piece of leather belt at the incisors.

2. Maximum incisal bite with a one-handed anterior pull

The addition of a single-handed anterior pull to an incisal bite has been used in this study to represent splitting of plant material, as described in early ethnographic accounts (Molnar et al 1972). A leather belt was used for this test also, as it is more suitable for resisting the forces of the test.

In preparation for this experiment, the digital spring gauge was securely attached between two sections of the leather belt. The hook of the gauge was inserted through the belt hole located on the “mouth” section, while the other section of the belt was threaded through the handle of the gauge to facilitate pulling by the participant.

For this test the participant was asked to bite down on a piece of a leather belt placed at their incisors as hard as they comfortably could whilst pulling horizontally (anteriorly) as hard as they comfortably could with their left hand. The left hand was used to pull in this test in order to try and avoid picking up any muscle activation from the pull itself.

3. Maximum incisal bite with a two-handed anterior pull

A two-handed anterior pull was also tested to represent the making of cordage or tightening of knots, a behaviour seen in Inuit communities (Molnar et al 1972). The leather belt was also used for this test.

For this test the participant was asked to bite down on a piece of a leather belt placed at their incisors as hard as they comfortably could whilst pulling horizontally (anteriorly) as hard as they comfortably could with both hands.

4. Maximum incisal bite with a one-handed downward pull

Changing the direction of the anterior pull to be more vertical was a test that aimed to represent the very common hunter-gatherer behaviour of defleshing hide (Molnar et al 1972). As the leather belt is made from hide, it was used for this test as well.

For this test the participant was asked to bite down on a piece of a leather belt placed at their incisors as hard as they comfortably could whilst pulling downward as hard as they comfortably could with their left hand. The left hand was used to pull in this test in order to try and avoid picking up any muscle activation from the pull itself.

Figure 4.09 Image of participant biting on a piece of leather belt at the incisors whilst pulling anteriorly and downward.

5. Maximum incisal bite with a two-handed downward pull

A two-handed pull directed downward and anteriorly was also tested in this study to represent the behaviour of stripping bark for spear shafts, as seen in Aboriginal Australian tribes (Molnar et al 1972). The leather belt was also used for this test to avoid the participant ingesting any unwanted plant matter and to avoid damage to the teeth.

For this test the participant was asked to bite down on a piece of a leather belt placed at their incisors as hard as they comfortably could whilst pulling downward as hard as they comfortably could with both hands.

Each of these tests were again repeated three times to reduce the impact of anomalous results, and the mean of these results were used where appropriate. It should be noted here that the synthetic leather snapped during the first pull, and so repetitions for this task could not be carried out.

Once all of the raw behavioural data had been collected, the post experimental protocol was followed. This meant carefully removing the electrodes from the participant and their disposal. The participants skin was then cleaned with soap and water to remove any remaining adhesive and equipment such as the load cell was disinfected.

4.3.4 EMG Data Analysis

The EMG data was collected and analysed on the programme MyoResearch XP Master Edition 1.08.17 as it complements the MyoSystem set up and is able to perform all of the tasks necessary for this study.

Before performing the analysis, the EMG signal needed to be processed. The frequency of the signal was set to a minimum of 25Hz and a maximum of 500Hz with a finite impulse response of 79 points. The signal then needed smoothing with a window of 50ms and was given rate monotonic scheduling. These setting are as described in the protocol outlined in Thomas Baird's (unpublished) 2025 thesis.

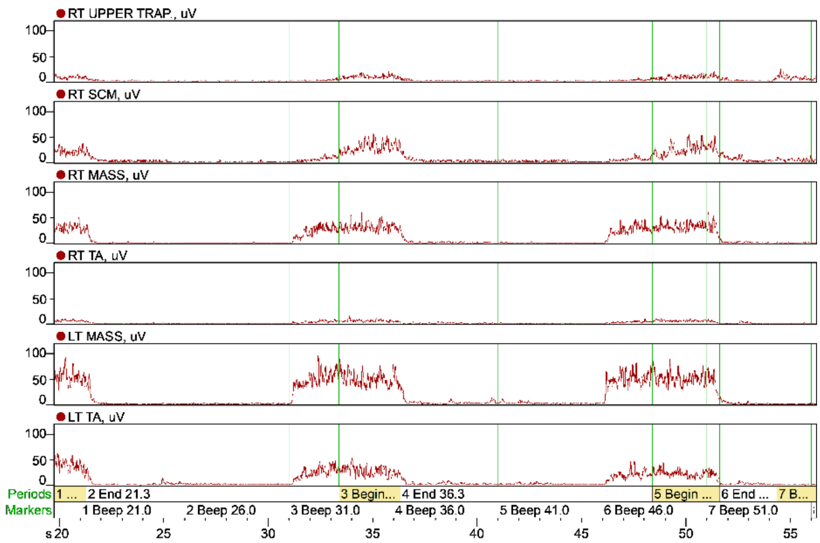

Figure 4.10: Image of processed EMG signals produced by the participant during behavioural test number one.

There are multiple ways that EMG data can be analysed, for the purposes of this study, the electrical signals were processed using average activation. The periods of analysis were defined as any rise/fall of 40% with a minimum duration of 0.5 seconds. These settings allowed the programme to pick up the three defined periods in which the participant was completing and repeating the tasks.

It is common for EMG researchers use the mean or the average values from the EMG signals for each muscle and so the mean values of each muscle activation during the five behavioural tasks have been used in this study (Valkeinen et al 2002; Hellmann et al 2012).

Because the muscle activation is measured as electrical activity (μV), it first needs to be "normalised" in order to be compared for both the male and female FE models and converted for use in FE models. For this, the maximum voluntary contraction tasks provide the highest values for each muscle, the mean EMG signal values are then divided by this maximum value for each muscle to create a percentage activation (Halaki and Ginn, 2012). These percentage activations are easier to convert and compare among various individuals and tasks.

The spring gauge used to measure the force of the anterior pulls in the behavioural tasks was set to measure in kilograms and so the results also needed to be converted into newtons for use in the FE model iterations.

4.3.5 Finite Element Analysis

As a suitable female FE model was made in chapter 3, it will serve as the starting point for the models needed for this chapter.

Following the methods outlined in chapter two, a male FE model was created for testing in this chapter to account for intraspecific variation, as if differences in strain patterns are consistent across both specimens when a particular modelling variable is altered, that variable is likely the cause. If the strain responses diverge, anatomical variation between individuals may be the contributing factor.

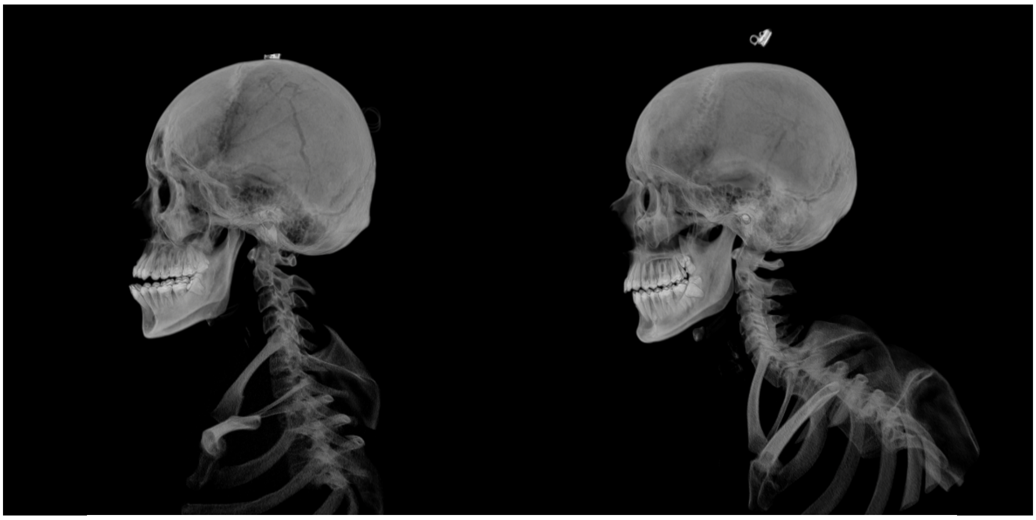

Fig 4.11: Volume renderings of original female specimen (left) and additional male specimen (right) (opacity setting: 0.15%).

Analysis of lateral and frontal views of the transposed volume renderings highlights dimorphic craniofacial characteristics. In the lateral projection, the male specimen exhibited a more sloped forehead contour, a larger occipital region, and a flatter cranial vault compared to the female. The male mandible was longer in the anteroposterior direction and featured a more prominent chin. Dental alignment differed between specimens, with the male presenting an overbite and the female an underbite. The male also displayed a larger nasal structure, with the nasal bone projecting in a near-horizontal orientation.

Fig 4.12: Transposed volume renderings of original female specimen and additional male specimen in frontal (left) and lateral (right) view (opacity setting: 0.065%).

Frontal view comparisons revealed that the female had a taller and asymmetrical cranial vault, while the male demonstrated more robust zygomatic arches. The male nasal cavity was vertically elongated but narrower in width, and his orbital region appeared larger than that of the female.

These morphological variations will need to be accounted for when comparing any differences in strain patterns and magnitudes produced by the FE models in this chapter, in order to correctly interpret the effects of EMG data and anterior pulling force inclusion.

The first model to be tested in this chapter will be based on the occipital condyle model from chapter two, with EMG data used for the masticatory muscle values, no neck muscles will be included.

For this chapter five biomechanically accurate FE models will be created, aligning with the five behavioural EMG tasks performed by the participant:

1) Static - incisal bite with *in vivo* masticatory and neck muscle force values
2) Anterior 1 - incisal bite with *in vivo* masticatory and neck muscle force values, and a onehanded anterior pull.
3) Anterior 2 - incisal bite with *in vivo* masticatory and neck muscle force values, and a twohanded anterior pull.
4) Down 1 - incisal bite with *in vivo* masticatory and neck muscle force values, and a onehanded downward pull.
5) Down 2 - incisal bite with *in vivo* masticatory and neck muscle force values, and a twohanded downward pull.

The first steps to creating the behavioural FE model iterations were to adjust the muscle activation values. Starting with iterations NM0 (incisor bite) and NM5 (incisor bite with an anterior pull), the muscles were given new values corresponding to the muscle activation percentages collected from the EMG behavioural tasks. The splenius capitis was removed from the models as it was deemed unnecessary in research by Giannakopoulos et al (2013) and also surface EMG methods are not considered appropriate due to significant interference of electrical signals from adjacent muscles (Mayoux et al., 1995).

As it was not possible to include the semispinalis capitis (SSC) in the EMG study, muscle activation percentage was calculated using information from Giannakopoulos et al 2018. Both the male and the female SSC muscle forces were adjusted to 15% of the fmax calculated using the methods outlined in the previous chapter, as per their coactivation percentage during a jaw clenching activity.

Table 10: Male and female semispinalis capitis muscle activation values to be used in FE models.

Specimen	fmax	15% activation
Male	231.069N	34.66N
Female	140.896N	21.13N

The rest of the masticatory and neck muscles were given different forces for each iteration, calculated from the activation percentages collected in the behavioural EMG tasks. The medial pterygoid was given the same activation percentage as the masseter muscle for each iteration based on findings from Schindler et al 2006. Reddy et al (2024) and Yin et al (2024) found that there was no significant difference between muscle activation percentage of males and females during various neck extension/flexion/bending tasks, and so there is no scaling required when using the male EMG percentage data for the female FE model.

Once the muscle forces were correct for each iteration, the anterior pull needed to be adjusted to ensure accurate testing. The force recorded for the pull during EMG behavioural tasks was different for each iteration and so needed to be adjusted in VOX-FE. The direction of the force also needed to be adjusted, as seen in the image below the anterior pull is directed forwards, whilst the downwards pull is directed at a lower angle.

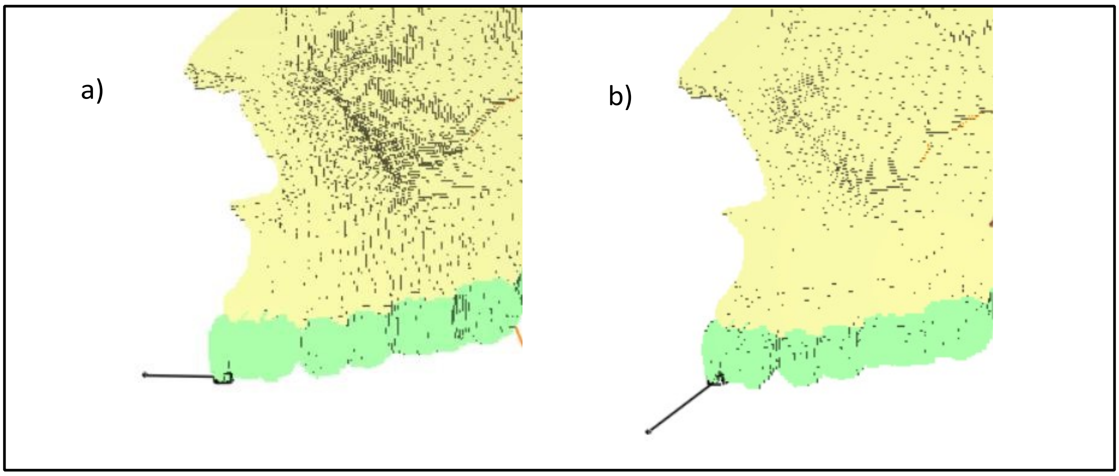

Figure 4.13: Direction of pull difference between a) anterior and b) downward iterations.

The strain extraction points were kept the same as the previous chapter so as to collect comprehensive craniofacial strain data for each behaviour. The models were then solved using the VOX-FE model solver (PARA-BMU) on Viking, then the nodal displacement files were imported back onto VOX-FE, to be viewed as a global strain map.

4.4 Results

The EMG results show that adding an anterior pull reduces activation of the primary masticatory muscles compared with a standard incisal bite and that neck muscle responses differ systematically with both the presence and the direction of that pull (see table 09).

The reduction in muscle activation when an anterior pull is present can be seen for the masseter and temporalis and is likely reflected in the deeper medial pterygoid as well. An anteriorly directed force on the mandible moves the condyles and changes the mandibular lever arm, increasing length of the jaw-closing muscles and altering their length–tension relationship. This mechanical shift reduces the need for high activation during occlusion, so activity in those muscles falls when the anterior pull is applied.

The sternocleidomastoid is known to contribute to head flexion, rotation, and to stabilising the atlanto-occipital joint during mandibular tasks. The anterior pulling force on the mandible changes the head–neck moment required to stabilise the mandible and hyoid complex (Jones., 2023). When an anteriorly directed force is loaded at the mandible, the bite force decreases, so the sternocleidomastoid muscle doesn’t need to work as hard to help stabilise the head and neck. Using two hands to apply the pull reduces the effort even further, which explains the gradual reduction in sternocleidomastoid activity seen in the EMG results.

The upper trapezius helps to lift and rotate the scapula and also supports the back of the neck. When the mandible is subjected to an anterior pulling force, the forces travelling through the head, neck, and thoracic spine changes. This places more strain on muscles that help stabilise the neck and shoulders, including the upper trapezius. As a result, the trapezius becomes more active to help manage these shifting forces. However, because this muscle also moves the scapula - especially when the arms are raised - its increased activity during a two-handed pull might partly be due to shoulder movement rather than just the need to stabilise posture. This means the EMG readings could be influenced by both the muscle’s role in holding the head steady and its involvement in moving the arms, which complicates the interpretation of the data.

Altering the direction of the pull increases sternocleidomastoid activation and reduces upper trapezius activation. A different pulling angle changes the moment arms around the atlanto-occipital joint, so muscles that are better suited for the new stabilising angle increase their activation. Sternocleidomastoid, with a line of action well oriented to resist an anterior–inferior shift and to control head rotation, becomes more active when the pull direction demands craniocervical control. Upper trapezius activation falls because the new angle reduces the need for much scapula movement.

Overall, the pattern is consistent with a redistribution of stabilisation between the masticatory muscles and the cervical and scapular muscles driven by changes in mandibular position and external pulling forces. An anterior pull reduces bite-related activation for masseter and temporalis while shifting stabilising loads to neck and shoulder muscles. The balance between sternocleidomastoid and upper trapezius activation depends on the pull's magnitude and direction.

All of the finite element model iterations shown in the following results have varying muscle activations in accordance with the EMG results. This should more accurately predict the biomechanical responses in the craniofacial region during various biting activities than in current anterior dental loading literature.

Bite force was tested using three bites on a load cell with a gape of 15.2mm. This produced results of; 278.7N, 250.6N, and 247.1N (average: 258.8N, standard deviation: 14.13N). This reduction in each bite is likely due to fatigue, as maximal biting requires a lot of force, and thus energy, from the participant. Upon learning of this difference, it would be suggested that in future testing bite force should be measured between each behavioural task, so as to keep a record of the changes in bite force during the session as there may have been further reduction throughout testing as the participant fatigued, which would likely have an increasing effect on results with each behavioural task.

4.4.1 Virtual Modelling with In Vivo Data

The first step to testing biomechanical responses to biting behaviours was to identify if there were any effects on strain from estimated versus real life muscle activations. As seen in the global strain maps below (figure 4.14) the estimated 50% masticatory muscle activation in both the male and female control model iterations predicted a difference in strain pattern when compared to the varied muscle activations that were calculated using the EMG data.

Table 11: Percentage activation of each muscle during five behavioural EMG tasks that are used to calculate muscle force in FE model iterations.

	Percentage Activation				
	Task 1	Task 2	Task 3	Task 4	Task 5
Masseter	44	36	33	44	43
Temporalis	64	33	24	20	19
Medial Pterygoid	44	36	33	44	43
Sternocleidomastoid	45	25	20	29	24
Trapezius pars descendens	52	65	100.5	46	40

The incisal bite simulations showed clear differences depending on both the type of model used and the sex of the individual. Models that used muscle force data from *in vivo* testing (Standard Model) produced higher bite forces - 196 N for the female and 238 N for the male - compared to models based on cadaver data (Control Model), which generated bite forces of 121 N and 179 N respectively. These differences were also reflected in the strain patterns observed on the skull. In the Standard Model, strain was more concentrated in key areas such as the zygomatic arch and nasoalveolar region, suggesting stronger and more focused loading during biting. In contrast, the Control Model showed lower and more diffused strain, indicating less intense force distribution. The male model generally showed higher strain than the female model, consistent with known differences in muscle size and bone structure. Overall, these results suggest that using *in vivo* muscle activation data leads to more realistic bite force predictions and strain patterns.

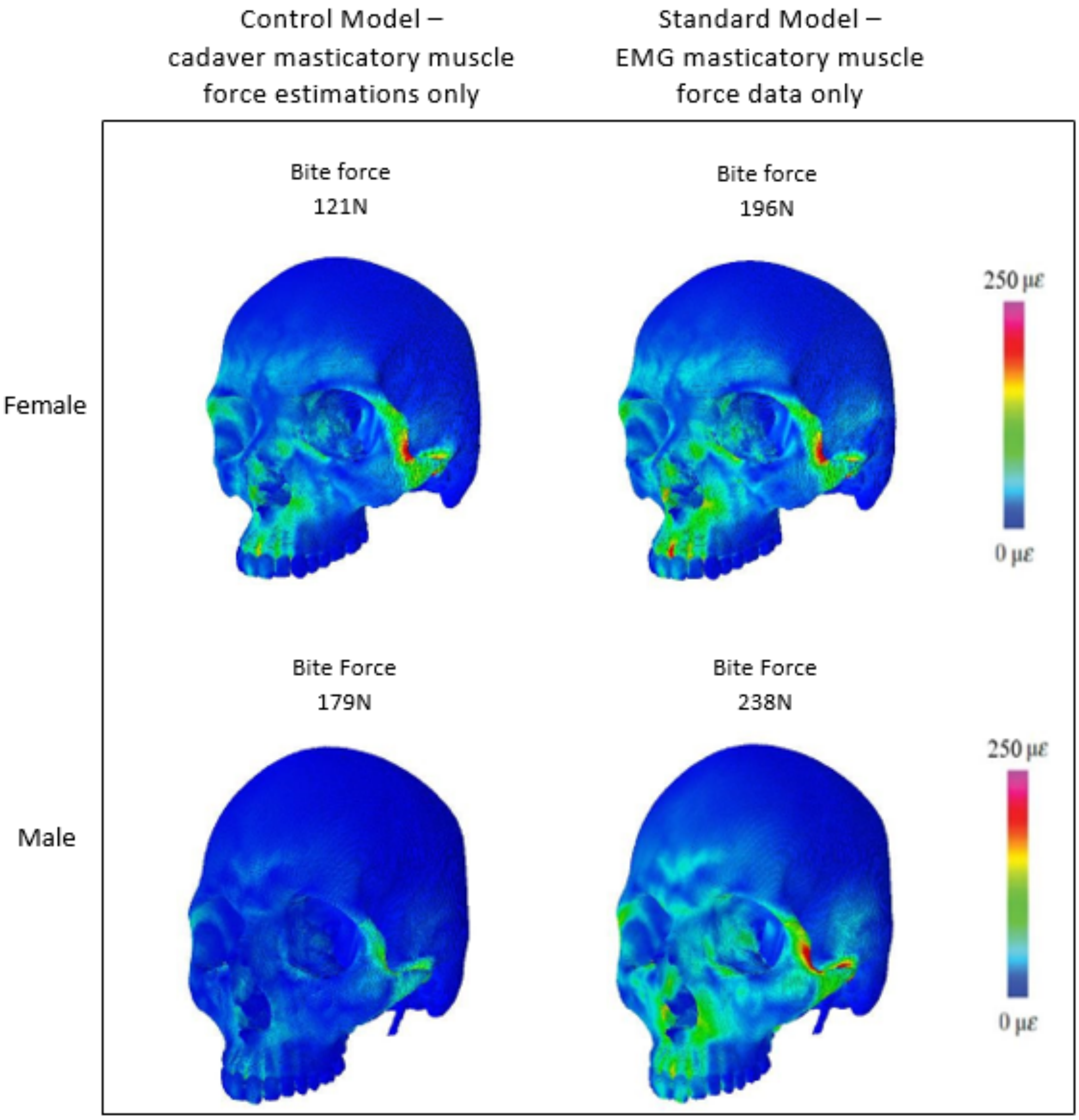

Fig 4.14: Strain contour plots of incisor bite models. The first models (left) have estimated muscle activation for the masticatory muscles (as seen in chapter 3) and the second models (right) have masticatory muscle activations calculated from the EMG task data.

Since these results established that muscle activation has a large effect on the craniofacial strain, the EMG data was then used to calculate the muscle activation for the sternocleidomastoid, upper trapezius and semispinalis capitis for both the male and female models. This iteration was labelled as “static bite” as it presents a standard incisal bite that would be seen in current published data, but with the addition of neck extensor muscles. This was then compared to the neck muscle model from the previous chapter which was loaded with neck muscle data from cadaveric estimations.

When comparing the global strain maps of the these iterations below, it can clearly be seen that a unique strain pattern emerges for each one (figure 4.15). This demonstrates the importance of detailed parameters when creating virtual reconstructions of bite scenarios, as this suggests that neck muscles play an important role in balancing forces in the skull when biting.

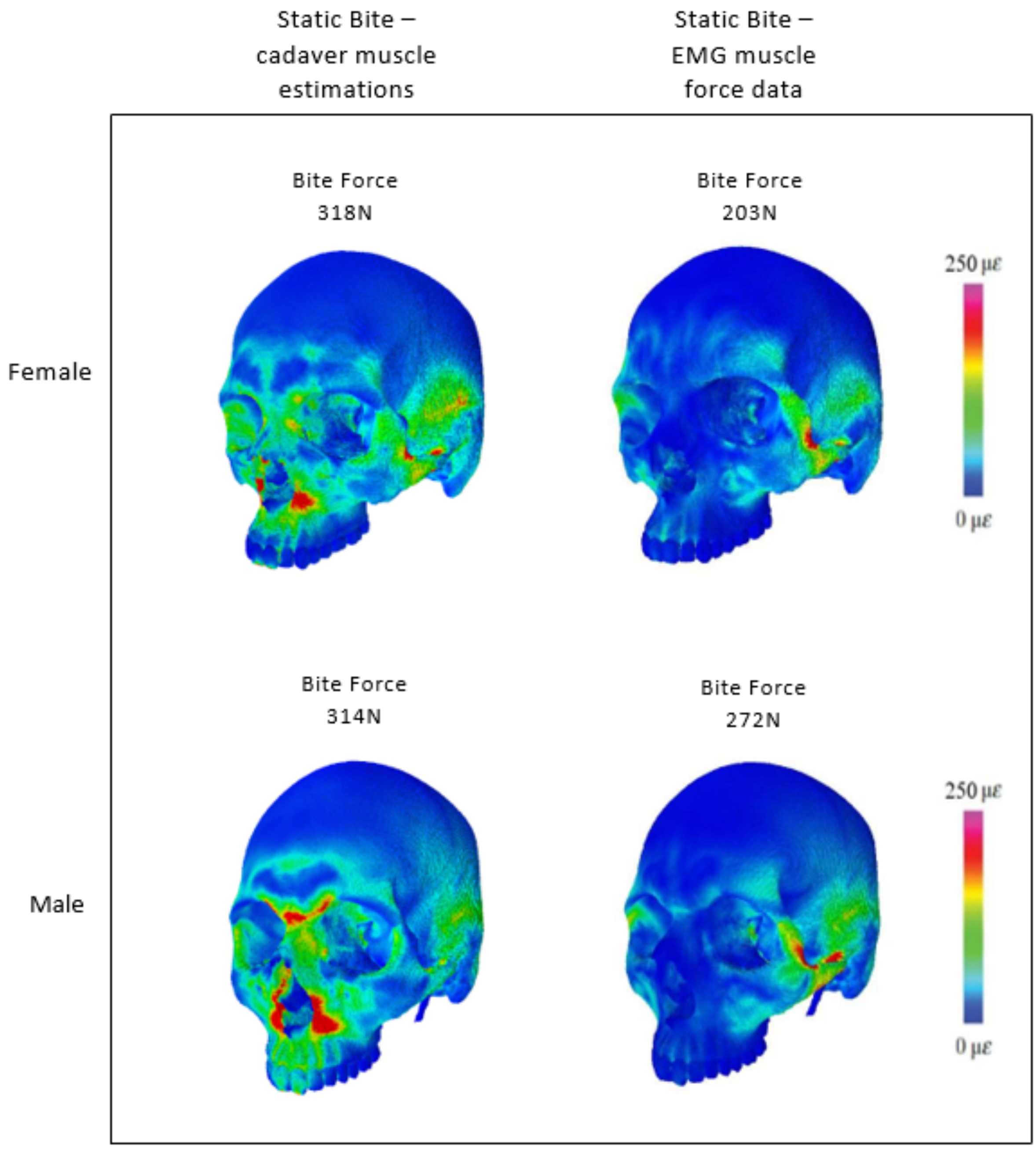

Fig 4.15: Strain contour plots of static bite models. The first models (left) have estimated muscle activation for the masticatory and neck extensor muscles (as seen in chapter 3) and the second models (right) have masticatory and neck extensor muscle activations calculated from the EMG task data.

Across both the cadaver and the EMG based models, strain magnitude was high in the zygomatic and temporal regions, which is expected as they are structurally involved in transmitting masticatory loads. In the male models, the broader and more robust zygomatic arches exhibited higher strain concentrations, particularly in the cadaver-based simulations, where bite forces exceeded 300 N. This suggests that a more robust zygoma may allow for greater force transmission, resulting in larger strain magnitudes. Notably, the EMG-based models displayed less pronounced strain patterns in the midface across both sexes, with reduced intensity and more localised peaks in strain magnitude.

When analysing the changes in the bite forces of these models, it is important to refer back to the bite forces produced by the participant in the bite force recordings. The participant performed three maximal incisor bites on a load cell: producing 278N, 251N, and 247N respectively. Although the variation between repetitions is moderate, the coefficient of variation of 6.3% is deemed acceptable in previously published literature as it is within the range of 5-10% (Edmonds & Glowacka, 2020). When comparing the *in vivo* bite forces (259N average) to those predicted by the FE models, it is clear to see that the male model with neck muscle activations derived from EMG data produced the most similar bite force (272N). This similarity between the *in vivo* recordings and the EMG based simulation suggests that implementing neck musculature as well as real-life muscle activation data may enhance the accuracy of the model, supporting its applicability for predicting functional bite performance in humans.

4.4.2 Static Bite vs Anterior Pull

When looking at the global strain maps of the static bite versus the bite with an anterior pull (figure 4.16) it is clear to see that the inclusion of the anteriorly directed force changes the craniofacial strain pattern. The higher strains appear in more central positions for the anterior pull model (incisors, glabella, central alveolar, and nasal margin) while the areas of high strain seen in the standard model are reduced in the anterior pull model (infraorbital region, zygoma, temporal region). The predicted strains are also much higher on the palate and palatal surface of the incisors when the anterior pull is added to the male and female models.

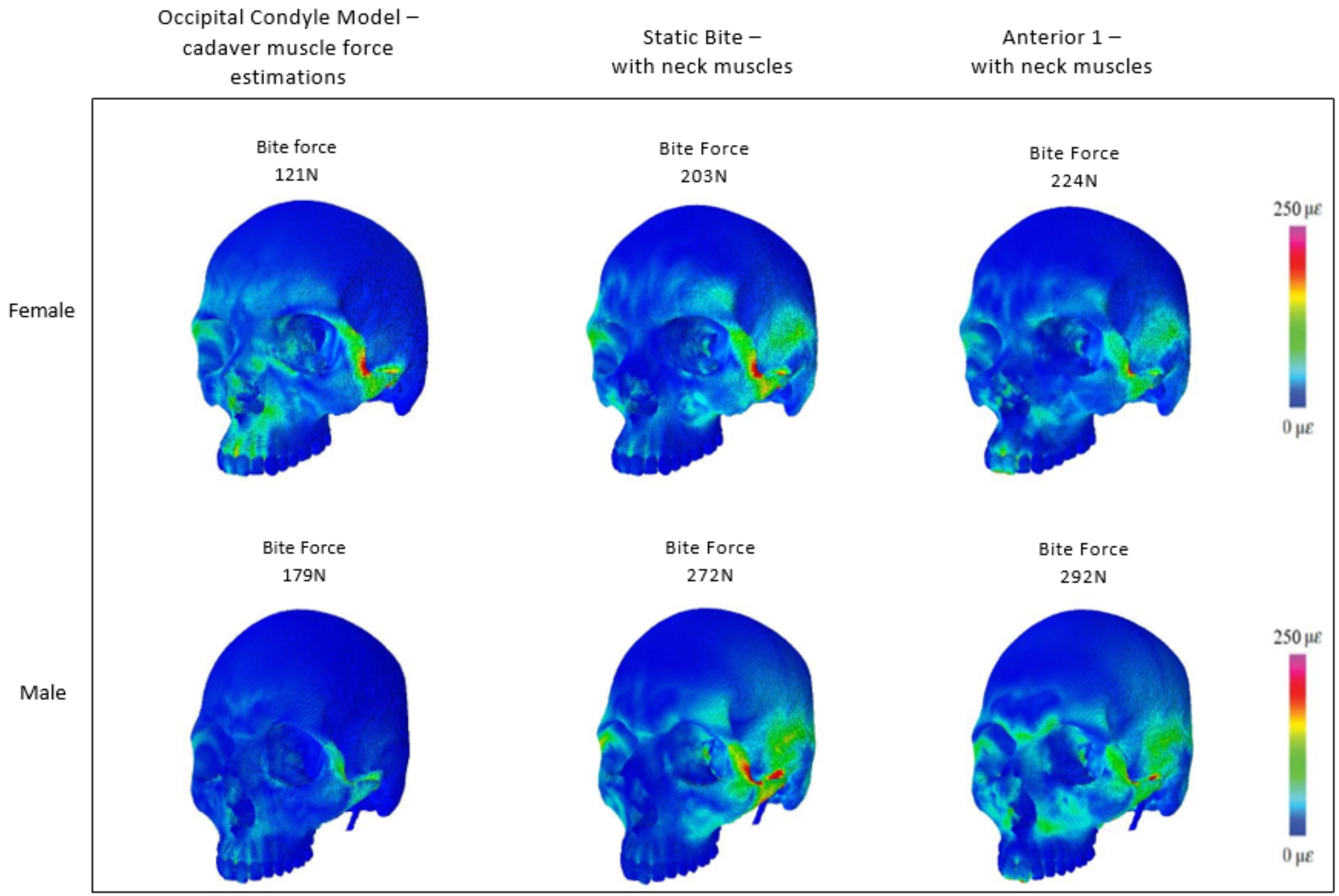

Fig 4.16: Strain contour plots of static bite and anterior pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data, the third models also have EMG derived neck muscle data with the addition of a one-handed anterior pulling force (133.861N).

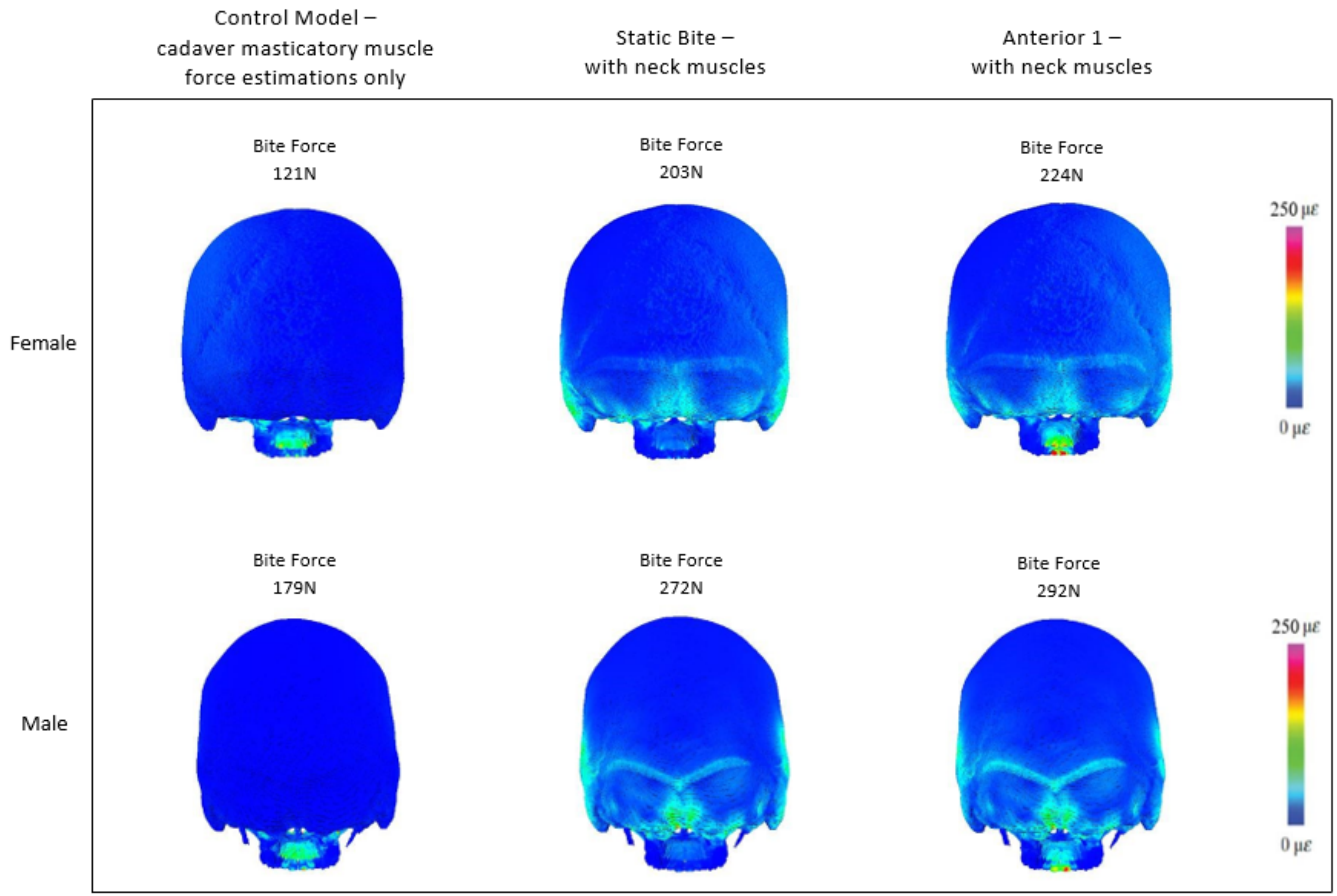

Fig 4.17: Occipital view of strain contour plots for static bite and anterior pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data, the third models also have EMG derived neck muscle data with the addition of a one-handed anterior pulling force (133.861N).

When comparing the Static Bite and Anterior 1 models, a reduction in strain at the mastoid process was observed for both the male and the female models when the anterior pull was included. This change in loading vectors alters the mechanical demands placed on the skull, shifting strain away from posterior regions such as the mastoid process and toward more anterior structures (the midface). The mastoid process serves as a key attachment site for the sternocleidomastoid and splenius capitis. In the Static Bite scenario, these muscles are more actively engaged to counteract vertical forces, resulting in elevated strain at the mastoid. However, the anterior pull in the Anterior 1 model recruits muscles differently and shifts the strain forward, reducing the mechanical load transmitted through the mastoid region. This change shows how the direction of forces relates to cranial morphology altering strain responses, particularly in areas associated with muscle attachment and load transmission.

The Static Bite model bite force was around 20N lower than that of the one-handed anterior pull model for both the male and female simulations. This increase likely occurred because the anterior pull helped to stabilise the head and neck, allowing the jaw muscles to work more effectively. By improving stabilisation and engaging additional supporting muscles, the jaw is able to generate more force at the bite point. These results suggest that head posture and external forces can influence bite performance, even during seemingly simple biting tasks.

Table 12: Standard deviation of internal and external strain at six craniofacial regions for male and female static bite and anterior 1 models.

	Female		Male	
Landmark Group	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Supraorbital Ridge (1, 2, 3)	29.80	11.29	30.50	9.01
Zygoma (4, 8, 9)	100.31	35.28	45.60	67.98
Temporal (5, 6)	39.57	16.52	15.07	14.58
Nasoalveolar (11, 12, 13, 14)	21.84	25.00	36.93	16.62
Occipital Region (15, 16, 17, 18, 19)	11.93	8.35	15.34	11.09
Posterior Maxilla (20)	64.20	17.59	24.24	1.61

The standard deviation of both internal and external strain for the Static Bite and Anterior 1 models is exhibited in table 10. The zygoma was the site of the biggest change for both the male and the female models, particularly landmark eight (zygomatic angle) on the female model. The internal strain in the zygomatic region appears to be more consistent for the male model, with a similar drop in strain at all three landmark points when an anterior pull is added. However, the external strain is more affected in the male model with a large change at landmark nine (temporal process) likely due to the temporal process acting as a key site for muscle attachment and force transmission during anteriorly directed loading. The external surface of the zygoma is more exposed to tensile forces generated by the anterior pull, whereas internal regions may distribute strain more efficiently, resulting in less pronounced changes.

As expected, the posterior maxilla and temporal regions were also areas of larger change for the female model. Loading an anteriorly directed force increased strain in the posterior maxilla, with visibly higher strain magnitude compared to the Static Bite model. This increase likely reflects the redistribution of force toward posterior structures as the skull resists both vertical and anteriorly directed loading. The temporal region also showed elevated strain, suggesting greater involvement of muscles for head stabilisation when counteracting the anterior pull.

4.4.3 Static Bite vs Downward Pull

The global strain maps of the Static Bite versus the Down 1 model clearly show that the inclusion of the downward pulling force changes the craniofacial strain pattern more subtly than the anterior pull, as the areas of high and low strain remain the same but the magnitudes differ. For example, the strain in the alveolar region is increased when a downward pull is added, but the zygoma and temporal regions are predicted to experience less strain.

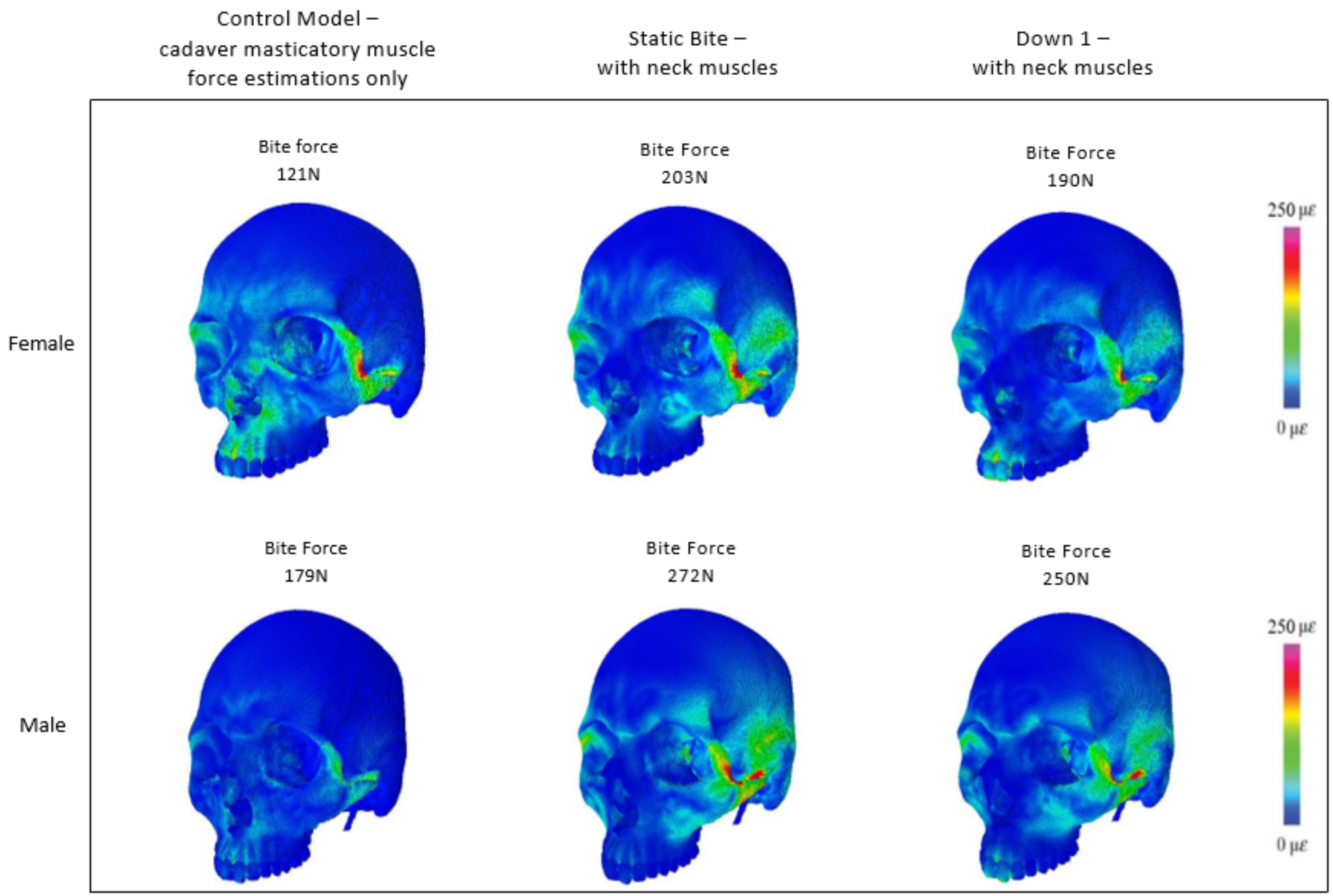

Fig 4.18: Strain contour plots for static bite and downward pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data, the third models also have EMG derived neck muscle data with the addition of a one-handed downward pulling force (155.926N).

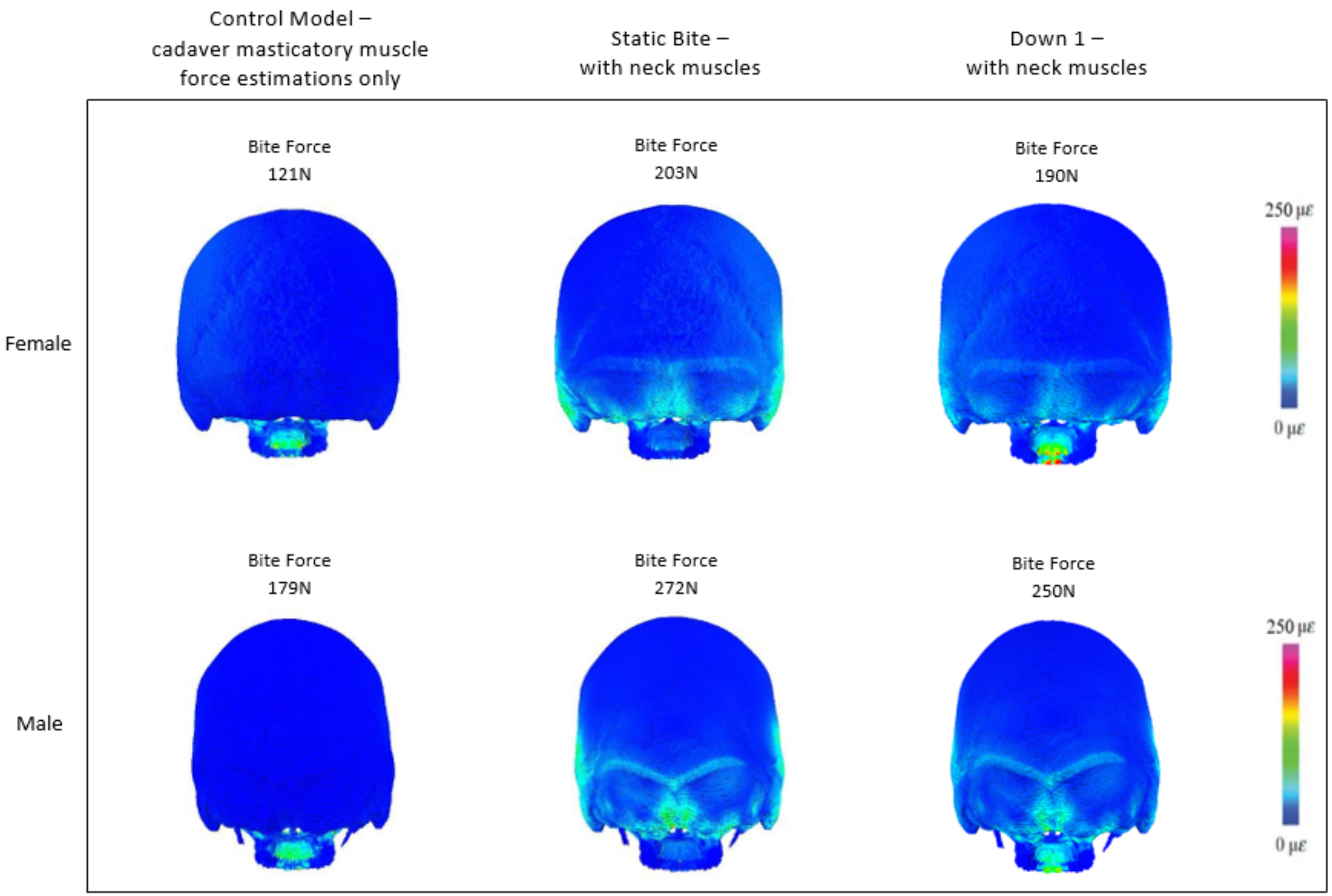

Fig 4.19: Occipital view of strain contour plots for static bite and downward pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data, the third models also have EMG derived neck muscle data with the addition of a one-handed downward pulling force (155.926N).

When comparing the Static Bite and Down 1 models, a reduction in strain at the mastoid process was observed for both the male and the female models when the downward pull was included. This same change in strain magnitude was observed for the Anterior 1 model as well. Visually, the pattern of strain remained largely the same, with the main changes resulting in decreases of strain magnitude in most regions. There was however an exception at the alveolar region, which saw an increase in strain both on the anterior and the posterior portion when the downward pulling force was added.

The Static Bite model bite force was higher than that of the one-handed downward pull model for both the male and female simulations. This decrease likely occurred because the downward direction of the pulling force is closer to opposing the upward force of the mandible than the anterior pull, which limits the bite force available for incisal occlusion.

Table 13: Standard deviation of internal and external strain at six craniofacial regions for male and female static bite and down 1 models.

	Female		Male	
Landmark Group	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Supraorbital Ridge (1, 2, 3)	29.36	11.28	29.44	7.87
Zygoma (4, 8, 9)	99.97	34.01	43.19	69.02
Temporal (5, 6)	39.96	16.56	16.26	14.11
Nasoalveolar (11, 12, 13, 14)	18.37	26.69	35.61	17.03
Occipital Region (15, 16, 17, 18, 19)	12.06	9.32	16.04	10.00
Posterior Maxilla (20)	68.53	24.20	31.67	16.79

The standard deviation of both internal and external strain for the Static Bite and Down 1 models is exhibited in table 11. The pattern of results here is very similar to that of the standard deviation of the Static Bite and Anterior 1 models. The zygoma was the site of the biggest change for both the male and the female models, although the effect of the pulling force appears greater for the female model than the male model. Again, the external strain is more affected in the male model with a large change at landmark nine (temporal process).

As was the case for the Anterior 1 model, the posterior maxilla and temporal regions were also areas of larger change for the female model. Loading a downward force increased strain in the posterior maxilla, with visibly higher strain magnitude compared to the Static Bite model. This increase likely shows how non-occlusal loading alters force distribution, as the alveolar regions attempts to resist the pulling force whilst also managing the vertical bite force. The temporal region showed elevated strain for the female Down 1 model, however very little change was predicted here for both internal and external strain for the male Down 1 model.

4.4.4 Changing the Magnitude of the Pulling Force

At first glance it looks as though adding a second hand to an anterior pull creates an incredibly drastic change in craniofacial strain (see figure 4.20). However, it is hard to gauge the true impact that the addition of a second hand has had on the craniofacial strain as the upper trapezius activation increased by over 35% compared to the one-handed pull, as it was the only muscle to increase so dramatically it was concluded that it was likely caused by the role that the trapezius plays in the pull itself (elevation of the scapula), rather than head stabilisation.

During EMG testing, a one-handed pull was conducted with the left arm whilst the electrodes were attached to the muscles on the right-hand side of the body. This eliminated the issue of recording activation from the upper trapezius elevating the scapula as the hand was raised to pull the belt from the mouth. However, this issue was not possible to avoid with a two-handed pull, research into techniques that could be used to prevent this in future testing would be necessary.

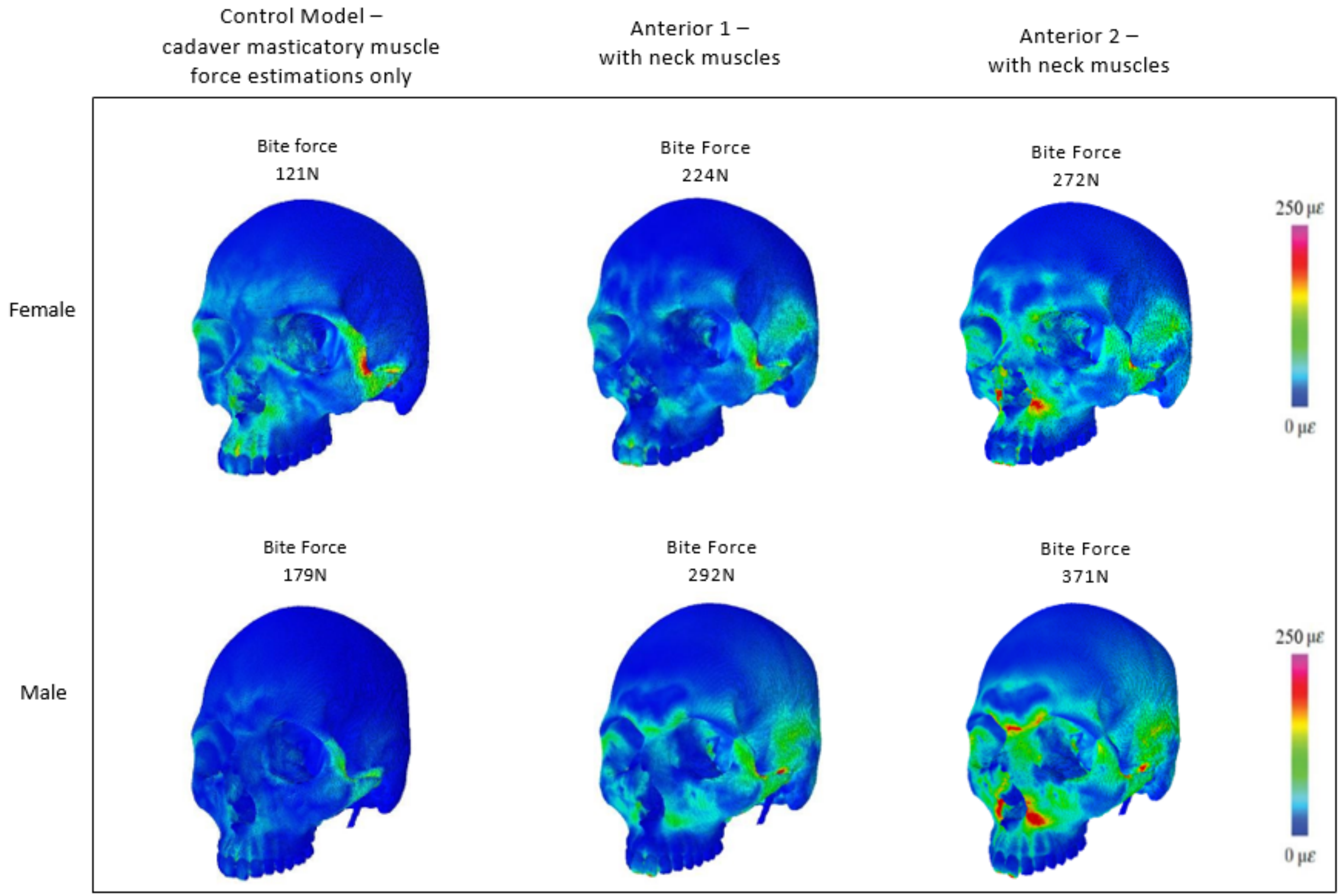

Fig 4.20: Strain contour plots for one and two-handed anterior pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data with the addition of a one-handed anterior pull (133.861N), the third models also have EMG derived neck muscle data with the addition of a two-handed anterior pulling force (134.645N).

When looking at the strain maps, it is hard to determine which changes in strain have been caused by the addition of the second hand to the anterior pull as intended, and which have been changed by the increase in activation of the trapezius unrelated to the stabilisation of the head.

The bite force also increases dramatically when a second hand is added to the anterior pull. Again, it is hard to determine how much of this increase came from the additional pulling force, versus the additional trapezius activation.

However, this was not an issue when conducting the two-handed downward pull test, as the arms were not raised, and so these results of the change in magnitude are more easily interpreted.

When adding a second hand to the downward pull, the changes to craniofacial strains appear much more subtle than in previous comparable models. When viewing the global strain maps (figure 4.21), there is a slight increase in strain in the alveolar region and small reductions in strains can be seen in the zygoma and temporal regions. In this case, the use of the strain extraction points and bite forces are more helpful to identify changes more easily.

The one-handed downward pull produced a higher bite force than that of the two-handed downward pull model for both the male and female models. Despite the similarity in visual strain patterns, the change in bite force was noticeably different for both the male and female iterations, with the two-handed pull reducing the bite force of the female model by around 15N and the male model by around 45N. This reduction might be due to the addition of a second hand to the pull engaging the neck extensors more, diverting the brain’s focus from the incisor bite to the stabilisation of the head.

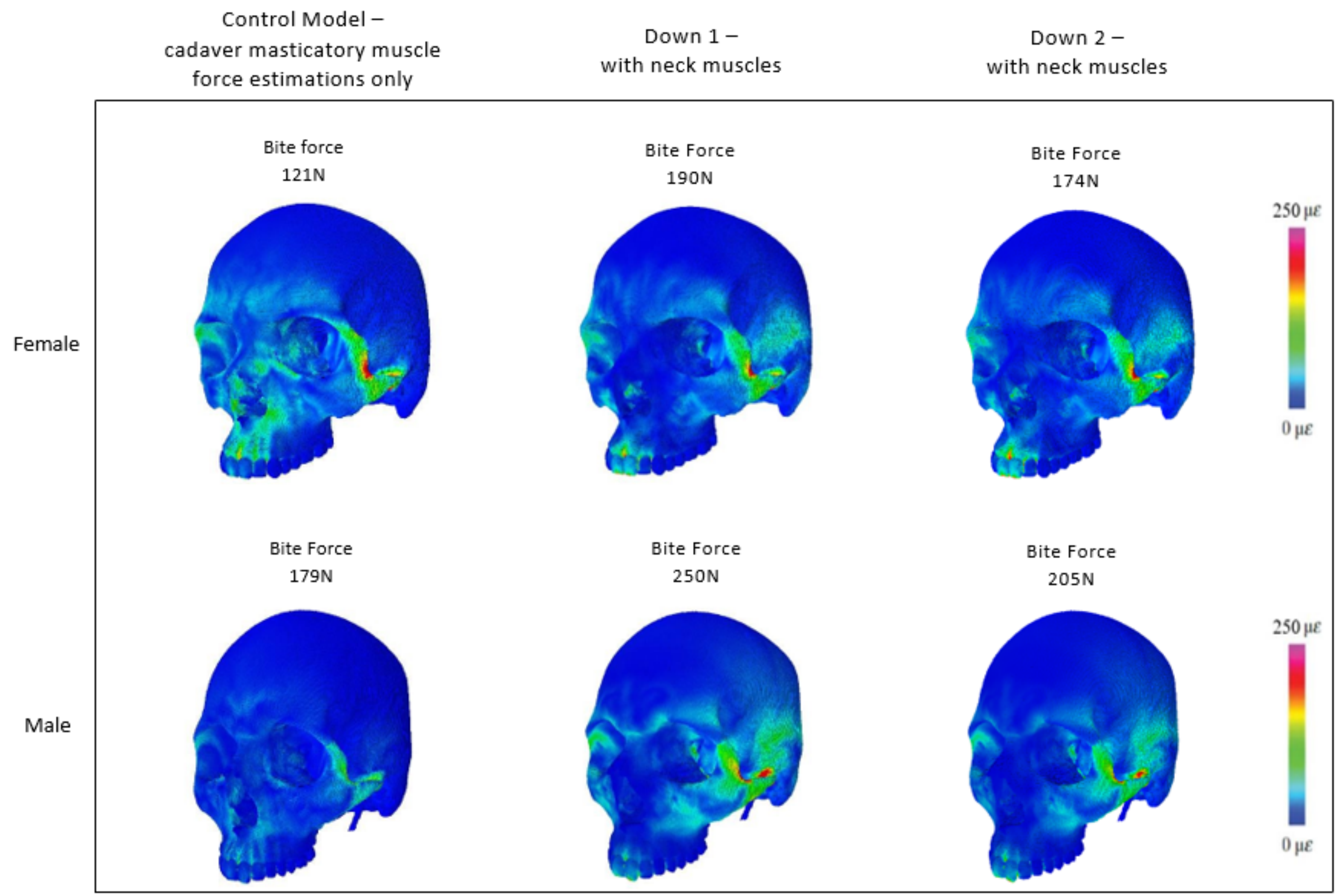

Fig 4.21: Strain contour plots for one and two-handed downward pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data with the addition of a one-handed downward pull (155.926N), the third models also have EMG derived neck muscle data with the addition of a two-handed downward pulling force (157.887N).

Table 14: Standard deviation of internal and external strain at six craniofacial regions for male and female down 1 and down 2 models.

	Female		Male	
Landmark Group	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Supraorbital Ridge (1, 2, 3)	21.02	7.52	21.35	5.551
Zygoma (4, 8, 9)	77.62	25.05	39.29	56.89
Temporal (5, 6)	31.88	9.58	7.89	12.21
Nasoalveolar (11, 12, 13, 14)	24.17	25.66	49.91	15.94
Occipital Region (15, 16, 17, 18, 19)	8.12	7.5	10.07	7.73
Posterior Maxilla (20)	9.08	11.47	7.10	3.89

Similar to other standard deviation results in this chapter, the zygoma and temporal region were the sites of the biggest change for the female model, both for internal and external strain. This was the same for the external strain for the male model, however the largest change in internal strain was in the nasoalveolar region.

The increased downward pull force appears to lead to an increased overall strain in the female model, but a decrease in overall strain for the male model (see tables A1 & A2 in appendix). This could be due to differences between the male and female models such as their muscle attachments or craniofacial morphology, which will be explored further in the discussion portion of this chapter.

4.4.5 Changing the Direction of the Pulling Force

Strain extraction points showed a decrease at the superciliary arch, temporal region, midface, nasal margin, and nuchal region when the direction of force was changed from anterior to downward (see tables A1 & A2 in appendix). However, the male model saw a much larger change in strain at the glabella than the female model, and the female model was predicted to experience a larger area of strain in the alveolar region in comparison to the rather compact reaction for the male model.

The changes in craniofacial strain are subtle when shifting the direction of the pull from anteriorly to downward, however they are there (see figure 4.22 below). The male and female models both predicted the same change in patterns for internal strains, with the downward pull increasing strains on the zygoma and the nasoalveolar region, compared to the anterior pull. The midface, glabella and temporal region all show less strain in the downward pull iteration. The increases in strain are likely a result of the higher pulling force managed by the participant in the downward pull task, whilst the areas of decreased strain are potentially linked to biomechanical adaptations since a the change in angle would change the way in which the force is dissipated through the skull.

The change in direction of the pull reduces the bite force for the male and female models by approximately 40N and 30N respectively. This change is likely due to the fact that the masticatory muscles work together to bring the mandible in an upward and slightly anterior motion. Therefore, when the anterior pull is added it complements the natural movement of the jaw, but when a downward pull is added it contradicts this movement and resists the bite and reduces the force it can produce.

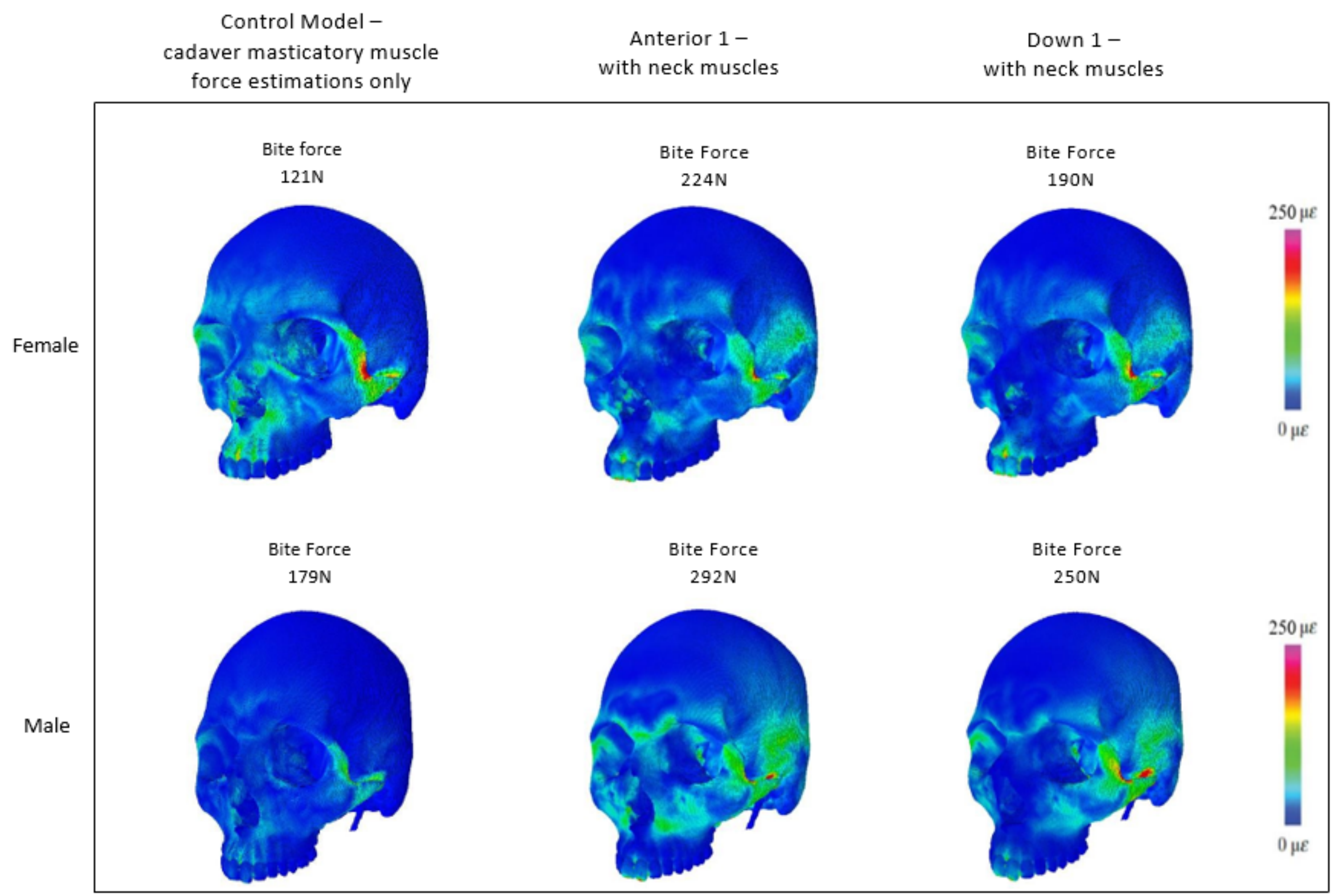

Fig 4.22: Strain contour plots for one-handed anterior and downward pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data with the addition of a one-handed anterior pull (133.861N), the third models also have EMG derived neck muscle data with the addition of a one-handed downward pulling force (155.926N).

Both the male and female models experienced a decrease in average internal strains when the direction of the pull was changed to be less anterior (see tables A1 & A2 in appendix). However, the magnitude of the difference was quite small, as average strain for the female model reduced by only 0.4 microstrain (με) and the average strain for the male model reduced by 3.3 microstrain (με).

As mentioned previously, there was an issue when recording the EMG signals for the anterior two-handed pull task as the upper trapezius was likely recording a higher activation based on its role in the elevation of the scapula which would be necessary for the anterior pull. Because of this the differences in strains cannot be reliably compared between both two-handed iterations. The changes in strain patterns are similar to those seen when comparing the Anterior 1 and Anterior 2 models, where the two-handed anterior pull showcases a higher level of strain across the entire facial region, and a significantly higher bite force (see figure 4.23).

This activation/recording issue would need to be investigated further before future research in order to determine which realistic behaviours can be reliably tested in this kind of loading scenario.

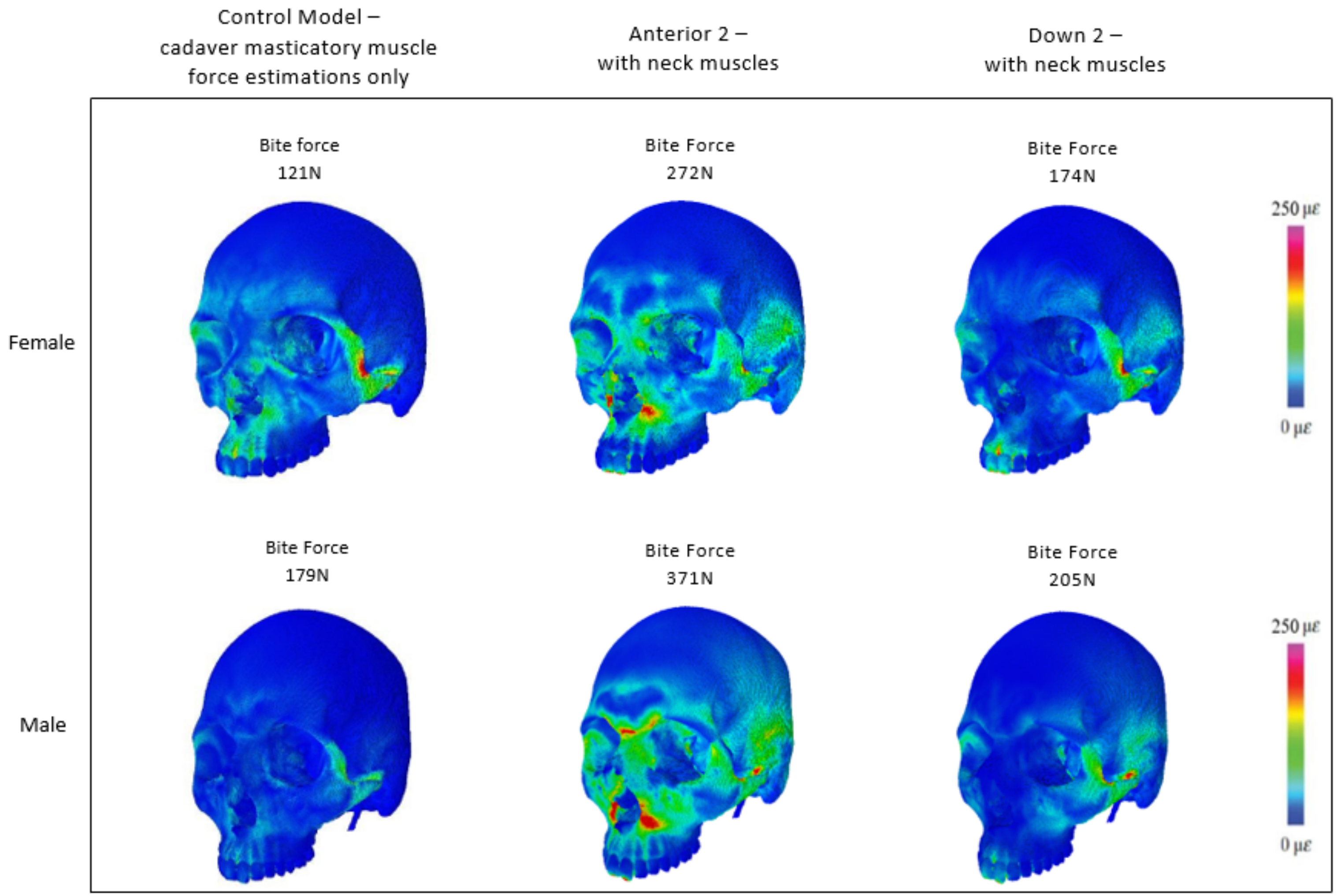

Fig 4.23: Strain contour plots for two-handed anterior and downward pull models. The first models (left) have estimated muscle activation for the masticatory muscles only (as seen in chapter 3) the second models (centre) have masticatory and neck extensor muscle activations calculated from the EMG task data with the addition of a two-handed anterior pull (134.645N), the third models also have EMG derived neck muscle data with the addition of a two-handed downward pulling force (157.887N).

Table 15: Standard deviation of overall internal and external strain for comparative models.

	Female		Male	
Comparative Models	Standard Deviation (ε_1)	Standard Deviation (ε_3)	Standard Deviation (ε_1)	Standard Deviation (ε_3)
Static Bite : Anterior 1	60.83	27.03	40.27	37.67
Static Bite : Down 1	64.56	29.11	43.05	39.72
Anterior 1 : Down 1	53.43	23.21	37.97	34.61
Down 1 : Down 2	57.15	25.72	39.81	34.52

When analysing the overall changes in craniofacial strain for the male and female models, it can be seen in table 13 above that internal strains in the female models experienced the most change across the various loading scenarios. The external strain was less affected than internal strain for all male and female loading scenarios, although there was less differentiation between them for the male model.

The addition of an external force on the incisor bite appears to have more of an effect than altering the magnitude or direction of the force. The change in strain from the static bite model to the one-handed downward pull was the largest, but the change between the one-handed anterior and downward pulls was the smallest. This suggests that introducing a novel loading condition - such as an external pull - may change the typical strain distribution more than altering an existing force. The craniofacial structure is likely more sensitive to the external mechanical forces than to directional variation alone, particularly when the incisor acts as the point of force transmission.

4.5 Discussion

4.5.1 Chapter Overview

This chapter aimed to use surface EMG to quantify neck muscle activity in order to more accurately replicate the effects of varied anterior biting behaviours on craniofacial strain patterns. This required a participant performing varied biting tasks while having their muscle activity recorded via surface electromyography. Their muscle activation percentages were then scaled to the male and female FE models from the previous chapter which allowed for more accurate virtual predictions of the craniofacial biomechanical responses to varied biting behaviours.

The methods used in this chapter followed protocols outlined in Thomas Baird's (unpublished) 2025 thesis, implementing techniques such as using surface electromyography to record *in vivo* muscle activity to be used in virtual reconstructions. Five specific male and female behavioural iterations were then tested in a finite element analysis software, collecting bite force and strain information across the crania as a whole, and at specific points of interest.

The results of the virtual testing in this chapter will be discussed in more detail with literary context in the subsequent sections.

4.5.2 In Vivo Data and Virtual Reconstruction

This study collected muscle activation data for the major muscles involved with biting and head stabilisation behaviours, that were shallow enough for surface EMG methods. The tasks that were asked of the participant aimed to replicate behaviours known to ethnographic communities that could also be inferred to extinct *Homo*, such as fleshing hide.

These tests provided both expected and unexpected results, such as the sternocleidomastoid being more highly activated during a standard bite than during the pulling task. As this muscle is generally thought of as a neck extensor it was assumed that resisting head flexion would have been the primary activation behaviour, but this was not the case. This result reinforces the decision to include the SCM in the FE biting simulations as it is directly involved in even the standard bite, and as such would have an effect on the resultant strain maps.

These tests also shed light on issues such as which behaviours can be reliably tested. When using two hands to pull anteriorly the trapezius was very highly activated in such a way that seemed anomalous, this jump in activation was concluded to have been caused by its assistance in raising the scapula in order to produce the pull. This artificially raised the muscle activation during the behaviour and so the value could not be solely attributed to head stabilisation. Because of this, future research would need to take this into account when deciding which behaviours to recreate. Ethnographic behaviours such as biting on cordage to weave with both hands would likely not be an issue, but simulating a common behaviour such as tearing tough raw meat would likely encounter this artificial activation.

When the masticatory muscle EMG data was input into the FE models, it was interesting to see the profound effects that it had on the strain patterns. While it was expected that there would be an increase in strain due to the slight increase in muscle activation, the areas of increase aligned almost perfectly with the areas of interest in dental loading discussions. The brow ridge, midface, zygoma, and incisors all experienced visually significant increases in strains which potentially reopens these areas up to discussions about remodelling and adaptation to repeated or heavy anterior dental loading.

Since there is such a difference when realistic muscle activation is added, it would be expected that using *in vivo* data should be required when creating an FE model so as to ensure the model is as accurate as possible. Whilst this is a reasonable assumption for research on human specimens, this could prove difficult when modelling extinct species in paleoanthropological studies when *in* vivo muscle activation data is unavailable. However, published research such as Berthaume (2014) used EMG data from behavioural tasks like spear thrusting performed by human participants and used the muscle activation percentages for their Neanderthal models of humeri. Although the authors acknowledged that while their strain magnitudes may not be accurate, the strain patterns would be and so could still infer potential areas of bone remodelling from these tasks.

Neck muscle activation data from the EMG tasks were also input into the FE models which again created significant differences in the strain patterns. The results from these additional parameters suggest that like in other disciplines, neck muscles are essential to creating biomechanically life-like virtual biting scenarios that help to increase the accuracy of the models and their results. Like before, the change in the loading of the skull created changes in strain magnitude and pattern, in the key areas of interest: the incisor, alveolar region, midface, and zygoma. This reinforces the fact that the addition of neck muscles to incisal loading FE models may be essential to creating physiologically realistic strain predictions. Such improvements in modelling precision have direct clinical relevance, particularly in surgical planning, orthodontic interventions, and prosthetic design, where understanding localised strain responses can inform treatment strategies and help to improve anatomical integrity.

Another aspect of the results that confirm these findings, is the predicted bite force. The bite force generated by the participant during a static bite test was compared to those predicted by the various static bite models. It was found that the model with neck extensors included, and EMG data used for all muscles loaded on the model, predicted the most similar bite force. This, coupled with craniofacial strain patterns, suggests that the novel loading of neck muscles with the addition of *in vivo* muscle activation data, presents a more biomechanically realistic model which may be more suitable than current published models. Particularly for applications requiring precise results such as clinical work or surgical planning.

4.5.3 Modelling Paramasticatory Loading

A great deal of change in strain is already predicted, simply by changing the muscle activation and the muscles included in the FE models, but another variable that caused significant change in this study was the addition of an external pulling force. When loading the model with either an anterior pull or a downward pull, the results confirmed that loading the skull with a behaviour other than an incisal bite creates more changes in strain pattern, thus supporting the argument that more than one behaviour should be tested when trying to determine the cause of craniofacial adaptations or clinical issues.

The occipital region displayed increased strains when the neck muscles were added to the models, this change occurred both with and without the anterior pull but most importantly it could prove to be an influential factor in assessing cervical conditions such as neck pain caused by bruxism or finding the cause of the Neanderthal chignon (occipital bun). While the strains are not high in magnitude for the models in this particular study, if the behaviours that cause these patterns were repeated often enough, they could potentially have caused bone remodelling that resulted in the unique occipital presentation of Neanderthals.

These results raise important considerations regarding the role of individual morphological variation in modulating cranial strain responses. Human craniofacial anatomy is highly variable, particularly in features such as occipital curvature, and the size and orientation of muscle attachment sites. These differences can significantly influence how external forces - like anterior or downward pulls - are transmitted through the skull and cervical region. For example, individuals with a more prominent occipital protuberance or increased regional muscle volume may experience altered strain trajectories under the same loading conditions, potentially affecting mechanical impact.

This sort of variation can be seen between the male and female specimens used in this study. In earlier comparison of their Avizo volume renderings, multiple morphological variations were identified, such as differences in occipital shape and size, as well as varied zygomatic robustness. When carrying this information forward into the FE model analysis, it may help to explain differences in craniofacial strain patterns between the male and female Anterior 1 models.

This kind of variability has direct implications for clinical assessment. Conditions like bruxism or cervicogenic headache may manifest differently depending on skeletal architecture (Al Khalili et al, 2022). A patient with a posteriorly positioned foramen magnum or prominent external occipital protuberance might be predisposed to higher strain concentrations in the suboccipital region during clenching or forward head posture (Ocran, 2014). This highlights the importance of accounting for anatomical variation in biomechanical evaluations to support more personalised results.

4.5.4 Varying Paramasticatory Loads

The changes seen in the strain patterns when adding an anterior pull suggest that these models are sensitive enough to require multiple behaviours to accurately tell the story of an individual's morphological adaptations. This study began to test this scenario by changing the direction of the anterior pull and its force. The results of these tests showed that changing these parameters does in fact continue to change the strain patterns and as such confirms that current published research does not reflect the sensitivity of these models and thus may not accurately depict craniofacial reaction to anterior dental loading. This is particularly relevant when considering the diversity of human craniofacial morphology, variations in features such as facial projection, and muscle attachment mean that individuals may respond differently to the same loading conditions. Because of this, a single behavioural scenario (static incisor bite) may oversimplify the biomechanics for an individual's anatomical composition.

While modelling these variations on a fossil hominin skull might not prove that they were particularly well adapted to these behaviours, it cannot be said for certain that they were not until more behaviours have been tested. As some published models have shown that there may be plausible causes for certain hominin craniofacial adaptations other than anterior dental loading (Wroe et al, 2018), it may be more realistic to expect that modelling these varied behaviours may not decisively end debate but perhaps support the hypothesis that a combination of behaviours and environmental factors contribute to their unique craniofacial morphology. This is further complicated by the fact that fossil hominins exhibit distinct anatomical traits such as: robust midfacial structures, expanded nasal apertures, or prominent occipital features. These features may affect behavioural loading in ways not yet accurately depicted by existing models. Testing a wider range of behaviours across morphologically distinct specimens could help clarify whether certain features are adaptive responses or outcomes of unrelated functional demands.

An issue encountered in this study that researchers would need to be overcome when using EMG data to replicate various behaviours for FE models is the artificial enhancement of activation patterns due to the multi-purpose nature of neck muscles. As seen in this study a two-handed anterior pull could not produce reliable upper trapezius data due to the heightened activation likely caused by the elevation of the scapula. This kind of issue is difficult to manoeuvre, particularly in the case of the trapezius, as it has a significant effect on midfacial strain in comparison to the other neck muscles loaded on the models used in this study. As well as this, anatomical variation in trapezius morphology could further vary its effects on overall craniofacial strains. This means that even with consistent behavioural loading, individual differences in muscle characteristics may lead to diverse strain outcomes, complicating attempts to generalise findings across populations.

4.5.5 Results Summary

This chapter set out to test three hypotheses, together they would give insight into the future of finite element models relating to anterior dental loading and paramasticatory behaviours.

Hypothesis one speculated that *in vivo* neck muscle activity would vary significantly during different bite loads. The results presented in this chapter support this hypothesis as every muscle tested had different activations depending on the task performed, therefore this hypothesis was accepted.

Hypothesis two tested whether the addition of an anterior pulling force would increase craniofacial strain compared to a static incisor bite model. The results of the Static Bite and Anterior 1 models required a more nuanced comparison of overall craniofacial strain, with predicted increases at the incisors, nasoalveolar region, and glabella. However, some regions, including the infraorbital, zygomatic, and temporal areas were expected to show reduced strain in contrary to the original hypothesis. By examining the strain values produced at each landmark, the female result dictates that the hypothesis should be rejected as there was a reduction in the overall internal and external strain when an anterior pull was added to the model (see table A1 in appendix). However, the male results portray a slightly different story with a small increase in the overall internal strain and a decrease in external strain. This suggests that this hypothesis can neither be accepted or rejected entirely, as it may depend on the anatomical variation of the specimen being tested.

Hypothesis three suggested that changes to the external pulling force would cause global variations in strain, whilst changes to the direction of force would cause more localised strain variations. When examining the strain maps, the change in direction appears to have a greater effect on global stain patterns than the change in magnitude. However, when comparing global changes in strain values the change in magnitude had the greater effect. When looking at local strain values (nasoalveolar and posterior maxilla landmarks) the change in magnitude again had greater effect than the change in direction. Therefore, the results support the hypothesis that changing the magnitude of the pulling force will cause global changes in strain, although the effect on strain when altering the direction of the pulling force was not limited to localised regions.

In summary, the aim of this chapter was successfully met as data collected *in vivo* (surface EMG) was used to create multiple virtual FE models that portrayed strain patterns believed to be accurate to real-life biomechanical responses to paramasticatory tasks.

Chapter 5: Discussion

5.1 Evaluating the use of EMG data in Virtual Modelling

One of the aims of this thesis was to use muscle activation data collected from EMG signals to use as masticatory and neck muscle forces in a finite element model that could be used for behavioural testing. This aim was achieved as evidenced by the results displayed in chapter four, showing that muscle forces have a large effect on craniofacial strains and that precision when calculating muscle forces is important. The results gained from each behavioural EMG test gave unique values for each muscle, showing just how variable head and neck muscle contributions can be. This variability prefaced the changes in craniofacial strains seen in the FE modelling which supported the line of thinking that more than one behaviour should be tested when investigating incisal biting scenarios.

Like Berthaume (2014) this thesis found that using EMG data gave more accurate results than using scaled cadaver values, this is backed up by the comparison of the Static Bite model bite force with the similar *in vivo* bite forces generated by the participant during EMG testing. These results suggest that previously published human FE models may be underestimating craniofacial strains, particularly at the nasoalveolar, zygomatic, and temporal regions. Each of these areas are closely associated with the action of major masticatory muscles: the nasoalveolar region is influenced by pull of the temporalis, the zygomatic region handles loading from the masseter, and as the site of origin the temporal region directly reflects temporalis activation. The improved strain predictions in the EMG models in this chapter likely come from the fact that they incorporate *in vivo* muscle activation patterns and force magnitudes, which directly impacts the mechanical strains of these skeletal areas. This highlights the critical role of individualised muscle data in producing anatomically and biomechanically realistic strain distributions within craniofacial FE models.

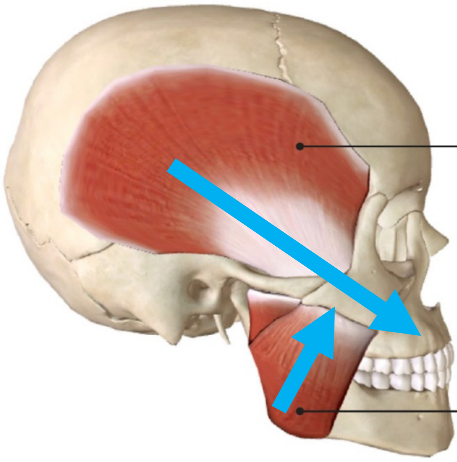

Fig 5.01: Diagram depicting direction of masticatory muscle forces (blue arrows).

Despite the positive results garnered from the EMG testing, it does have its limitations. For example, the problem encountered with the upper trapezius in behavioural test number three (two-handed anterior pull), where the activation was increased by over 35% in comparison to test number two (one-handed anterior pull). As this jump was almost certainly caused by the trapezius assisting with the elevating of the scapula, rather than with head stabilisation, it would be impossible to say how much of the activation was being used for head stabilisation and so it likely that future testing would encounter the same issue as the activations for these roles cannot be separated. As the craniofacial strain patterns were severely affected by this jump in muscle activity, it can be said that the upper trapezius is a major contributor for craniofacial loading. Therefore, further research on how to correctly record activation relating to only head stabilisation is important before it can be considered for use in behaviourally varied biting FE models.

The inclusion of masticatory and neck muscles forces derived from EMG data also presents time related constraints when applied in a clinical context. The individuality of the model requiring *in vivo* muscle activation data may be an unrealistic addition to routine patient pre- and post-surgical assessments. Asking a patient to perform EMG testing in advance of treatment planning, etc could be unfeasible due to both the time it takes to set up and record the data prior to modelling, and also the physical aspect may prove difficult for patients experiencing pain. These factors limit the feasibility of modelling with EMG data in clinical applications, especially when quick decision-making or patient comfort is prioritised.

Another issue with using EMG data in FE models within palaeoanthropology is that fossil hominin likely did not produce the same muscle activation percentage as humans during the same loading behaviours, therefore using human EMG data for these models would not be completely accurate. However, as shown in Berthaume (2014), fossil hominin models could be compared to a human model in the exact same loading scenarios to visualise the relative differences in resistance to forces, rather than drawing conclusions on the strain magnitudes themselves.

5.2 Evaluating the use of Neck Muscles in Biting Simulations

Another important question sought to be answered by this thesis was whether the inclusion of neck muscles would have an effect on the predicted craniofacial strain patterns produced by an incisor bite FE model. This question was answered successfully during the analysis of multiple models in chapters three and four. The results of the tests in this thesis showed that neck muscles do have an effect on the craniofacial strains of an incisor bite model, both individually and as a collective.

The results of this thesis strongly support the inclusion of neck musculature in craniofacial finite element models, particularly in clinical contexts where accurate strain prediction is essential. Models that included neck musculature produced varied strain distributions in the midface and nasoalveolar regions compared to models that did not have them. These differences suggest that stabilising forces from the neck muscles play a significant role in shaping craniofacial loading during biting, and their omission may lead to underestimation of strain within clinical contexts. For surgical planning or implant design, where understanding these strain patterns is critical, models that include neck musculature would present a more physiologically realistic representation of craniofacial biomechanics.

The results collected in this thesis showed a considerable difference between strains produced when no neck muscles were included versus when they were. The pattern of strain in the midface and alveolar region was completely changed by this addition and when comparing the chapter four Static Bite model with the human models published by Wroe et al (2018), the differences in strain patterns are striking. These comparisons suggest that published models may not be as biomechanically accurate as previously thought, showing that despite the variable nature of human craniofacial morphology the exclusion of neck musculature can lead to systematic underestimation or misrepresentation of strain in key areas such as the nasoalveolar and midfacial regions.

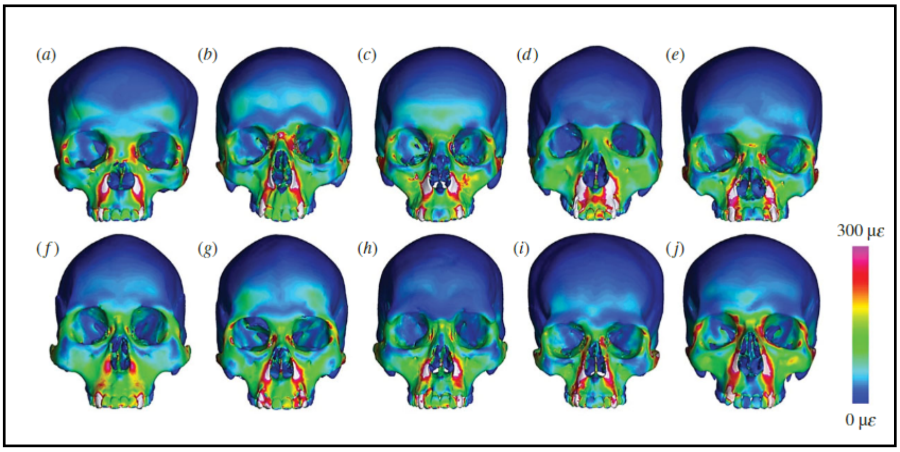

Fig 5.02: Cropped image of modern human resultant strain contour plots taken from Wroe et al, 2018 (pp. 4).

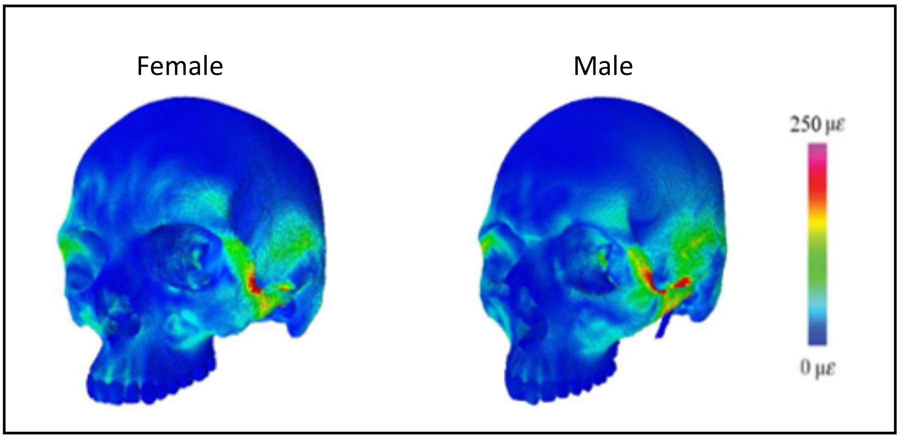

Fig 5.03: Strain contour plots of female and male Static Bite models with masticatory and neck extensor muscle activations calculated from the EMG task data, taken from chapter four results.

Another point of discussion arising from the inclusion of neck muscles is that while midfacial strains decrease, strains in the occipital region increase. This change is expected due to the muscle forces originating from this region, however as a point of interest that does not exist in previously published models, it does lend support to the idea that the robust occipital regions in hominins could have been influenced by anterior dental loading behaviours. As neck muscle attachment sites in the occipital regions of some extinct hominin are larger than humans it could be theorised that their predicted strains would vary significantly to that of the models presented in this thesis. Neck muscle testing on multiple hominin models would be needed to say this for certain, but would also be an interesting structural difference to examine.

Despite the overall optimism of the findings relating to neck muscle inclusion in this thesis, there are improvements that could be made if this research was to be repeated. Firstly, it would be beneficial to have EMG data for all of the neck muscles used for the FE model so as to further improve the reliability and anatomical accuracy of the results. Not having access to the semispinalis capitis due to the selection of the surface EMG method will likely have had some effect on the local strain magnitudes, particularly in the posterior portion of the skull. Nonetheless, the results gained from using neck muscles in the FE models are still valuable.

If this experiment were to be repeated, it could be of benefit to also test other neck muscles in order to build a more comprehensive understanding of how the neck extensors contribute to head stabilisation and craniofacial strains during incisor biting . By testing more neck muscles, it could also be said with more reliability which muscles have no impact on craniofacial strains and could be omitted from future models without affecting the accuracy of the results.

5.3 Evaluating the use of Varied Behaviours for FE Models

Discovering the effects of varying the behavioural scenarios loaded into the FE models was another key aspect of testing in this thesis. The results in chapter four showed that changing the behaviours modelled did in fact have an effect on the strains produced each time. This confirmed the idea that more than one biting scenario is needed in order to make any assumptions about an individual's craniofacial strain patterns or morphological adaptations.

The addition of a pulling force had the expected effect of increasing strain at the incisor and alveolar regions. Although the increase in strain magnitude at the alveolar region was lower than it was initially predicted to be. This may have been due to the antagonistic actions of the neck muscles, working to counterbalance the anterior force and as such, lowering the overall strain in that area. These changes highlight the complex relationship between the masticatory muscles and the neck extensors in determining craniofacial strain patterns.

Changing the direction of the pulling force had another large impact on craniofacial strain patterns, whilst increasing the pulling force had more of an effect on the magnitude of the strains. This demonstrates that the vector of the pulling force influences how the mechanical strains transmit through the skull, while the magnitude of the pulling force directly impacts the intensity of these strains. The main areas of variation in strain patterns appeared to be morphologies that are often associated with anterior dental loading research.

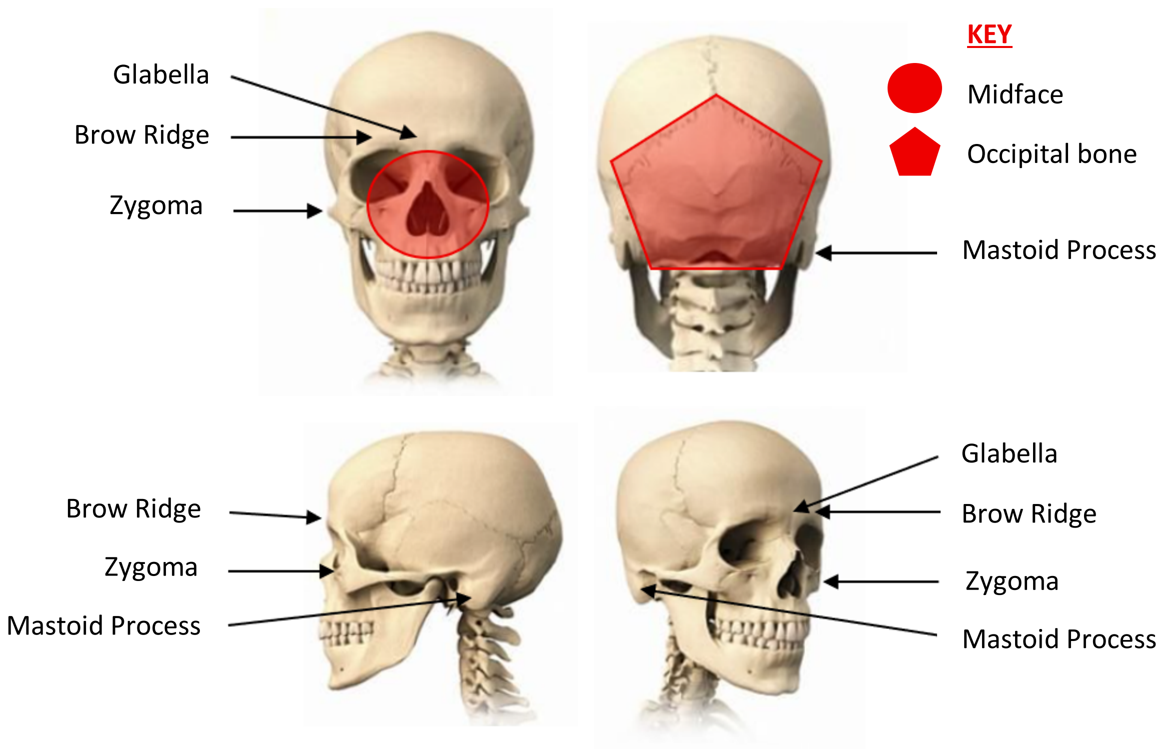

Fig 5.04: Four different orientations of the skull, labelled with the key areas of variation found in behavioural testing.

Morphological features such as brow ridges, glabella, zygoma, midface, mastoid process, and the occipital bone, all experience the largest changes across the various behavioural models tested in this thesis. From these results it would be reasonable to expect that changing the presentation of these features would have significant effects on craniofacial strain patterns. Therefore, when evaluating functional morphology or testing evolutionary hypotheses, it is essential to account for how variation in these regions may impact mechanical strains in varied incisal loading scenarios.

These findings carry important clinical implications, particularly for procedures involving the midface, zygoma, and nasoalveolar region. The sensitivity of these areas to changes in pulling force vectors and head stabilisation suggests that individual variation in craniofacial morphology could significantly influence post-surgical strain outcomes. For example, patients with more prominent brow ridges or zygoma may produce a different mechanical response to incisor loading than those with more gracile features. Including neck musculature in FE models appears to improve the accuracy of strain predictions, this would allow clinicians to better anticipate stress concentrations and potential failure points in reconstructive surgery, implant placement, or trauma management. This aligns with recent findings that emphasize the importance of active muscle repositioning and cervical stabilisation in biomechanical modelling of the head and neck, particularly in scenarios involving non-neutral postures or complex loading conditions (Hadagali et al, 2024).

While assessing changes in feature presentation will be important in future research, issues encountered in this study would need to be solved or avoided first. The issue encountered in behavioural test number three (two-handed anterior pull) would likely be present for other behaviours if the tests require arm elevation on the same side as the muscles being recorded. Therefore, in future testing this would need to be a key consideration when designing behavioural tasks in order to avoid artificial activation values.

With the introduction of varied behavioural loading, a key challenge will be to determine how many combinations of movements is enough to satisfy the full range of physiologically relevant loading scenarios. Accurately assessing an individual's ability to withstand forces generated by paramasticatory behaviours requires a balance between biomechanical diligence and practical feasibility. While it could be tempting to incorporate as many behavioural models as possible into a study, it would reduce its applicability in a clinical setting and have an inverse effect on the number of specimens that can be realistically analysed at any one time, particularly limiting in large or multi-species studies. For example, Wroe et al (2018) tested ten modern humans, three Neanderthals, and one Heidelbergensis specimen, if they were to run five behavioural tests on each (such as in this study), that would require seventy FE model iterations which would be a substantial amount of research both in terms of resources and workload. This implies a need for strategic model selection that would prioritise the most informative behaviours without compromising the accuracy of the results.

5.4 Future Research

Fundamentally, no research is without room for improvement, this passage will seek to determine possible directions for future research in order to further improve upon the methods used and results gathered in this thesis. Before expanding the research methods, the models used in this thesis require validation, in order to confirm that the findings reflect real life biomechanical behaviour and identify any potential modelling errors. Once these models have been validated, their use in wider clinical and paleoanthropological contexts could be encouraged.

The small number of specimens (n=2) and participants (n=1) in this study limits the certainty at which the results can be said to be reliable. With such a small sample, it cannot be confirmed that some changes seen in craniofacial strains were caused by the factors tested and not external factors such as variations in morphology or sexual dimorphism. This opens up another avenue of future research, which could look to investigate the impact of differences in craniofacial morphologies, both for intraspecific (human) and interspecific (hominin) variation. Knowing the extent of impact that can be caused by an individual's craniofacial variation would be particularly of use within clinical contexts requiring comparative elements.

Once validated and deemed reliable, the most logical next step for this research would be to test additional craniofacial musculature, in order to assess their impacts on strain patterns, determine which muscles are necessary to produce accurate models, and identify where the limit is to avoid overloading the models. Results from this kind of testing would further help to improve the balance of anatomical integrity and modelling efficiency, making it more suitable for practical applications by providing a clear muscular protocol capable of producing reliable results. To be able to test more muscles, methodology should also be assessed so as to collect muscle activation data reliably.

A primary consideration for improving data collection would be to use fine-needle (intramuscular) EMG instead of surface EMG in order to collect data from deeper and smaller muscles such as the medial pterygoid (Chen et al, 2017). Including *in vivo* data for the medial pterygoid and semispinalis capitis would likely increase the accuracy of the predicted craniofacial strains. Intramuscular EMG could also help to reduce the effects of artificial activation at the upper trapezius during behaviours that require elevated scapulae, however this would require sensitivity testing to be able to assess how effective it is.

Additional methodological changes that could help to strengthen the reliability of the models could include the use of magnetic resonance imaging (MRI) as the initial point of reference for the specimen. As an MRI is a higher resolution image than a CT scan, visualisation of the muscle attachments would be clearer, enabling better estimates of pennation angles, fibre orientations, and cross-sectional areas. Another helpful addition to the methodology would be geometric morphometrics (GMM), which allows for the quantification of changes in shape. This could be used to define boundary conditions, allowing for consistent muscle attachment placement and thus improving repeatability and integrity across multiple models. It could also be used to correlate strain patterns with changes in morphology, which would improve understanding of how craniofacial shaping affects strain.

Fig 5.05: Left; Man biting an apple requiring a large gape (stock image). Centre; Man cracking a nut using his canine teeth (Still from youtube video by Steviejacko, 2015). Right; Woman snapping off a beer bottle cap with her teeth (Hope Dental Clinic, 2021).

As discussed previously, changing the behaviours modelled had a large effect on strains and so testing more behaviours in future research could help to expand our knowledge of how the skull reacts to these varied forces. Changing the movement from a pull to a snap could be a valid loading scenario, as snapping objects such as small bones with the dentition is a fairly common ethnographic behaviour (Molnar, 1972). Altering the bites themselves may also be interesting as only the incisal bite has been tested in this thesis. Testing a canine bite could open up even more lines of investigation. Many paramasticatory behaviours can also be performed at the canine, with external pulling forces being directed laterally (Estalrrich & Marín-Arroyo, 2021). This would require a unilateral bite, which would consist of unbalanced loading of the musculoskeletal system, potentially presenting even more fascinating changes in craniofacial strain patterns.

Another variable loading test that could be incorporated in future studies would be change to the mandibular gape and to trial how its variance would affect the craniofacial strains. In this study a fully occluded bite was used, however, in real life objects used during paramasticatory loading would vary in size;

- Weaving cordage, this would be close to full occlusion with the gape likely being around 5-10mm (Turner et al, 1996).
- Fleshing seal hide, on average seal hide is around 25mm thick (Mellish et al, 2007).

Such a vast increase in gape would change the bite force considerably as the masseter and medial pterygoid become more stretched, it would also change the activations of the neck muscles as they work to balance out the “lever opening” of the TMJ.

Once the methodology and loading scenarios have been finalised, statistical testing would be a final logical step to validate their findings and compare patterns in a meaningful way. Repeated measure ANOVA would be useful to compare strain patterns and muscle forces across multiple loading scenarios for the same specimen. This would help to account for intra-specimen variability and test the relationships between specific factors, such as muscles loaded and bite location. Principal component analysis (PCA) would be particularly helpful if using GMM as it aids with analysis of shape variation and can help relate variation to biomechanical factors in larger data sets.

Chapter 6: Conclusions

The aim of this thesis was to investigate the role that the neck musculature plays in influencing craniofacial strain during biting behaviours. In particular, how paramasticatory loading behaviours, are likely to engage the neck musculature and thus alter craniofacial strain patterns. By integrating *in vivo* surface electromyography (sEMG) data with finite element (FE) modelling, this research assessed how the inclusion of neck muscles and more realistic loading scenarios influenced modelling outcomes and interpretations. This was done by completing the following objectives:

Building an FE model capable of simulating masticatory and paramasticatory loads with the addition of neck musculature was the first objective that needed to be completed for this study. Chapter 3 was composed of multiple sensitivity tests which sought to determine the most reasonable configuration of boundary conditions to accurately simulate incisor biting scenarios. Novel loads were also tested here in order to confirm that the desired mechanical effect was being produced. Although a sensible combination of constraint placements, anterior pulling force configurations, and neck musculature were selected, due to the time constraints of the study the final model was not validated.

The second objective of this thesis was to evaluate the impact of neck musculature on craniofacial strain patterns during anterior and vertical biting. This was tested in chapter 3, whereby the model was given neck musculature and loaded once with a vertical bite, and then with an anterior pull. Both loading scenarios predicted a large increase in global strains, particularly in the facial and temporal regions, when compared to the other sensitivity models in this chapter that were not given neck muscles. These results gave an insight into the potential effects of neck musculature on anterior dental loading models. However, more accurate muscle activations would likely provide more reliable data on the size of the impact that these neck extensors make.

The next objective to be completed was to record *in vivo* muscle activation data from masticatory and neck muscles during a variety of biting and pulling tasks using surface electromyography. This was completed in chapter four by collecting muscle activation data from a consenting participant during a vertical bite and varied anterior pulling tasks. The activation data was then loaded into a male and a female FE model. A vertical incisor bite model was then tested with and without neck muscles in order to determine the effects of cadaveric estimations versus *in vivo* activations. This testing also had a major limitation due to the multifunctional nature of the upper trapezius which recorded a large increase in activation when performing the two-handed anterior pull task, linked with its role in scapula elevation.

The final objective of this thesis was to apply these activations to FE models in order to test how more realistic loading conditions influence craniofacial strain distributions. This was completed in chapter four using muscle activation data gathered in EMG testing during multiple behavioural scenarios, which were then implemented for the male and female FE models. The effect of changing the direction of an external pulling force (anterior vs downward) and the impact of changing the magnitude of these pulling forces (one-handed vs two-handed) were analysed. This testing did have its limitations, as only one *in vivo* male participant was tested, so the activation data had to be scaled for the female model muscle forces, thus potentially affecting the reliability of the results.

By completing these objectives this study was able to address key questions posed in chapter one.

The primary question sought to be answered by this thesis was to what extent does neck musculature influence craniofacial strain predictions during anterior biting, and should they be considered a necessary addition to finite element analysis? Through sensitivity testing in chapter 3, this study demonstrated how four neck extensor muscles affected craniofacial strains both as a collective, and individually. As well as confirming that these muscles have a global impact on craniofacial strains, this study found that they improved the reliability of the model, strengthening the argument that their inclusion should be a key consideration when loading an FE model for an incisal bite.

The second question at the beginning of this thesis asked how changing the direction and nature of the anterior dental loading (vertical bite versus anteriorly placed pulling force) affects predicted craniofacial strain patterns. Chapter four tested various loading scenarios stemming from a bilateral incisor bite. These scenarios varied the direction and magnitude of the applied external pulling forces, simulating different muscle activation patterns and mechanical reactions. By comparing the bite forces, craniofacial strain patterns, and magnitudes produced by the various behavioural models, it was confirmed that altering the vectors of an external pulling force had a measurable impact. This change produced global differences in craniofacial strains when compared to the model loaded using the previous chapter's protocol.

The final question of this thesis asked how the use of *in vivo* activations to calculate muscle forces compares to using forces estimated from cadavers, in terms of predicted strain magnitudes and distribution. Comparisons were made both with and without the presence of neck extensors. Both the male and female models loaded with *in vivo* muscle data showed increased global strain magnitudes when only the masticatory muscles were present. When models with neck muscles loaded with either cadaveric estimation or *in vivo* data were compared, the predicted strains showed global changes in both magnitude and distribution. These results showed that the source of the muscle data had an effect on craniofacial strains, even more so when neck extensors were present. This information would prove incredibly useful in clinical settings requiring precise strain outputs.

This thesis has introduced novel finite element modelling approaches with the aims of more reliably representing the complexities of craniofacial biomechanics. These methodologies have provided numerous insights into functional load distribution across varied loading scenarios. They have revealed diverse strain patterns that challenge current published protocols and could help to improve the reliability of both clinical and evolutionary interpretations. By performing numerous sensitivity tests and trialling novel techniques, this study presents optimistic results for improved reliability in anterior dental loading research, but also calls for caution, until rigorous biomechanical validation has been carried out. Future research can build on these frameworks to explore dynamic loading scenarios, patient-specific modelling, and broader evolutionary comparisons in craniofacial form and function.

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Appendix

This appendix contains comprehensive strain data tables for the FE models of chapter four that I have not integrated into the results section, but I believe it is important that the reader still has access to this information (section A). It also includes the participant information sheet and participant consent form used for the chapter four EMG testing (section B).

Section A

Table A1: Principal strain 1 and 3 values (με) from each landmark for chapter four female models (see Table 03 and Figure 2.16 for landmark information).

Landmark Number	Standard Incisal Bite		Anterior Pull One Hand		Downward Pull One Hand		Downward Pull Two Hands	
	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3
1L	16.624	-8.651	15.504	-11.653	19.585	-9.614	21.708	-9.127
1R	12.826	-5.841	11.741	-6.456	14.996	-6.058	17.078	-10.805
2L	37.162	-9.441	41.272	-10.012	38.401	-10.427	34.509	-10.070
2R	47.989	-15.735	52.643	-17.865	49.876	-16.610	45.638	-15.641
3L	72.299	-29.746	54.610	-21.879	50.309	-20.846	45.031	-19.093
3R	113.565	-43.215	79.335	-31.812	81.977	-30.859	76.992	-28.115
4L	159.647	-54.256	92.109	-29.673	123.422	-40.975	124.735	-41.865
4R	116.167	-42.133	67.533	-26.760	88.003	-33.533	89.308	-33.384
5L	160.129	-65.414	136.249	-58.768	121.909	-55.139	113.336	-51.648
5R	94.766	-62.391	76.210	-53.848	66.081	-44.154	62.308	-41.434
6L	63.734	-37.545	58.397	-41.210	48.161	-40.442	44.240	-38.396
6R	48.452	-13.021	45.155	-34.511	36.274	-27.745	33.166	-25.854
7L	8.224	-5.534	14.988	-13.165	8.444	-5.361	16.470	-12.363
7R	2.433	-3.250	19.305	-11.297	2.084	-5.162	6.250	-14.922
8L	283.116	-116.727	172.706	-68.974	211.190	-85.867	207.000	-84.633
8R	348.727	-116.727	224.305	-82.680	263.999	-96.583	254.999	-93.066
9L	40.500	-128.735	28.255	-30.718	43.456	-34.251	45.807	-32.602
9R	52.898	-73.210	38.474	-34.076	63.831	-42.987	68.327	-42.865
10L	74.279	-67.724	59.999	-67.553	56.217	-61.515	46.974	-50.115
10R	38.545	-57.940	18.437	-34.844	21.106	-35.929	19.498	-31.388
11L	28.192	-71.592	77.841	-26.945	3.735	-6.419	14.496	-40.312
11R	40.514	-96.782	65.254	-28.148	3.607	-15.495	20.693	-51.338
12L	22.014	-41.842	10.096	-7.882	24.194	-29.407	31.972	-39.818
12R	17.678	-27.947	7.080	-5.091	18.418	-20.696	23.909	-27.789
13L	32.816	-31.162	55.970	-72.989	73.471	-89.003	84.853	-100.869
13R	22.303	-23.838	38.264	-52.626	51.253	-66.817	59.246	-76.085
14L	4.579	-16.896	6.356	-22.666	8.722	-33.326	10.362	-39.778
14R	8.349	-13.023	9.081	-22.697	14.527	-30.520	17.274	-35.011
15L	17.742	-13.608	10.300	-9.574	10.845	-8.536	9.388	-7.406
15R	23.771	-8.422	15.932	-6.523	15.248	-5.483	12.916	-4.606
16L	37.558	-17.759	30.178	-14.418	25.618	-11.838	22.704	-10.446
16R	60.037	-29.583	45.838	-22.264	38.830	8.283	33.367	-14.644
17L	35.963	-17.111	37.962	-19.178	28.027	-14.224	24.541	-12.645
17R	29.203	-22.810	30.037	-24.230	22.633	-17.817	20.173	-15.415
18L	30.661	-30.922	29.895	-30.025	17.152	-22.622	20.407	-19.711
18R	24.412	-17.045	22.313	-15.269	11.134	-11.286	14.853	-9.689
19L	12.407	-22.062	15.494	-27.053	11.134	-18.968	9.772	-16.315
19R	16.488	-31.533	19.169	-38.380	13.245	-26.109	11.053	-22.048
20L	24.890	-22.996	136.546	-57.394	144.639	-65.303	155.178	-71.863
20R	6.668	-35.287	149.834	-67.543	159.064	-84.315	170.037	-95.107

Table A2: Principal strain 1 and 3 values (με) from each landmark for chapter four female models (see Table 03 and Figure 2.16 for landmark information).

Landmark Number	Standard Incisal Bite		Anterior Pull One Hand		Downward Pull One Hand		Downward Pull Two Hands	
	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3	ε_1	ε_3
1L	4.433	-7.601	8.881	-12.333	5.647	-7.703	4.042	-6.735
1R	5.087	-4.899	5.457	-9.053	8.020	-8.981	8.478	-8.494
2L	45.161	-17.512	57.294	-35.749	47.996	-23.971	38.079	-17.301
2R	45.123	-18.921	36.673	-15.742	37.254	-15.613	29.946	-12.471
3L	80.028	-26.965	65.552	-21.695	61.341	-21.105	46.521	-16.215
3R	93.462	-30.104	74.481	-23.013	66.624	-20.846	49.332	-15.517
4L	85.111	-36.533	52.103	-20.675	64.226	-27.120	52.854	-22.400
4R	100.646	-31.957	44.891	-16.223	67.885	-22.127	56.620	-18.388
5L	80.827	-80.850	63.567	-78.900	54.900	-71.583	43.924	-58.158
5R	85.911	-44.291	68.098	-42.518	55.500	-39.400	44.769	-31.779
6L	49.708	-42.956	48.520	-48.100	41.633	-42.769	34.244	-35.951
6R	46.195	-53.672	45.364	-57.433	39.691	-50.551	32.624	-42.077
7L	22.619	-19.141	39.782	-16.796	18.623	-10.220	11.539	-8.612
7R	25.236	-13.680	48.902	-18.175	22.417	-8.232	13.643	-7.695
8L	167.222	-84.177	125.327	-55.416	149.944	-70.323	124.580	-58.379
8R	194.687	-71.114	149.622	-46.884	172.622	-58.384	141.649	-48.003
9L	164.615	-228.541	107.918	-167.247	124.098	-186.566	98.292	-151.634
9R	104.747	-183.126	70.352	-131.221	82.869	-151.970	66.490	-123.487
10L	31.970	-31.127	83.595	-83.336	64.171	-65.766	49.992	-51.732
10R	34.366	-27.170	54.916	-33.265	42.078	-27.052	31.467	-20.685
11L	20.818	-61.684	92.910	-27.444	14.589	-10.361	2.248	-6.533
11R	23.605	-49.773	119.880	-36.222	21.605	-12.080	3.630	-4.701
12L	6.206	-12.088	4.671	-4.453	5.072	-8.063	5.758	-9.474
12R	13.640	-28.256	3.546	-7.934	7.331	-13.474	7.849	-11.909
13L	55.395	-24.142	93.603	-23.457	143.287	-44.359	158.200	-50.066
13R	42.167	-20.270	35.750	-18.107	73.158	-40.770	83.004	-47.396
14L	4.946	-8.574	3.645	-3.518	6.509	-9.756	7.326	-11.212
14R	3.977	-6.466	2.495	-1.168	5.296	-6.888	6.149	-8.296
15L	78.432	-35.779	53.475	-22.786	49.077	-22.310	37.416	-17.153
15R	56.181	-26.630	37.588	-16.121	35.450	-15.521	27.084	-11.614
16L	46.698	-30.927	39.654	-23.984	33.696	-20.104	26.666	-15.404
16R	12.569	-13.029	16.086	-10.072	10.800	-8.927	8.418	-7.004
17L	31.727	-19.455	34.489	-20.900	26.084	-15.846	20.402	-12.469
17R	22.788	-39.339	24.386	-39.243	18.245	-30.082	13.924	-23.035
18L	29.860	-43.513	27.805	-42.710	21.980	-32.895	16.709	-24.858
18R	43.632	-41.521	42.984	-40.324	33.855	-31.236	26.106	-23.606
19L	20.896	-40.942	21.043	-46.553	16.472	-33.611	12.729	-24.222
19L	26.887	-37.004	27.571	-40.225	21.294	-28.907	16.267	-20.418
20L	23.662	-45.002	76.270	-48.014	91.639	-79.326	97.028	-86.442
20R	21.366	-43.617	64.144	-44.929	78.680	-76.281	83.474	-83.527

Section B

Below are the documents required for ethical approval of EMG testing as part of chapter four:

- HYMS Ethical approval application form submitted to the HYMS ethics committee and University of York, Department of Archaeology ethics committee.
- Participant information sheet detailing the purpose of the study and what may be required of them if they consent to take part, etc.
- Participant consent form highlighting that consent may be withdrawn at any time, and that personal information such as their name will be kept confidential, but images and data collected during the study will be published – though they will be anonymised.

HULL YORK MEDICAL SCHOOL

HYMS ETHICS COMMITTEE

APPLICATION FOR APPROVAL OF A PROJECT INVOLVING

HUMAN PARTICIPANTS, HUMAN DATA, OR HUMAN MATERIAL

This application form is to be used by researchers seeking approval from the **HYMS Ethics Committee**.

Applications to HYMS Ethics Committee, with the specified attachments, should be **submitted electronically to: ethics@hyms.ac.uk**

RESEARCH MUST NOT BEGIN UNTIL ETHICAL APPROVAL HAS BEEN OBTAINED

Please complete every section, using N/A if appropriate.

Incomplete forms will be returned to the applicant.

Office Use Only *(for final hard copies)*

Reference Number:

Date final copy received:

Approval decision:

Approved – no conditions ☐

Committee ☐

Chairs Action ☐

Expedited ☐

Approved with conditions ☐

Committee ☐

Chairs Action ☐

Expedited ☐

Declaration of the Principal Investigator/Supervisor and Student Investigator

- The information in this form is accurate to the best of my knowledge and belief, and I take full responsibility for it.
- I undertake to abide by the ethical principles underlying the Declaration of Helsinki and the HYMS good practice guidelines on the proper conduct of research, together with the codes of practice laid down by any relevant professional or learned society.
- If the research is approved, I undertake to adhere to the study plan, the terms of the full application of which HYMS Ethics Committee has given a favourable opinion, and any conditions set out by HYMS Ethics Committee in giving its favourable opinion.
- I undertake to seek an ethical opinion from HYMS Ethics Committee before implementing substantial amendments to the study plan or to the terms of the full application of which the HYMS Ethics Committee has given a favourable opinion.
- I understand that I am responsible for monitoring the research at all times.
- If there are any serious adverse events, I understand that I am responsible for immediately stopping the research and alerting HYMS Ethics Committee within 24 hours of the occurrence.
- I am aware of my responsibility to be up to date and comply with the requirements of the law and relevant guidelines relating to security and confidentiality of personal data.
- I understand that research records/data may be subject to inspection for audit purposes if required in future.
- I understand that personal data about me as a researcher in this application will be held by HYMS and that this will be managed according to the principles established in the Data Protection Act.
- I understand that the information contained in this application, any supporting documentation and all correspondence with HYMS Ethics Committee relating to the application, will be subject to the provisions of the Freedom of Information Acts. The information may be disclosed in response to requests made under the Acts except where statutory exemptions apply.
- I understand that all conditions apply to any co-applicants and researchers involved in the study, and that it is my responsibility to ensure that they abide by them.

- **For Supervisors**: I understand my responsibilities as supervisor, and will ensure, to the best of my abilities, that the student investigator abides by HYMS Policy on Research Ethics at all times.

- **For the Student Investigator**: I understand my responsibilities to work within a set of safety, ethical and other guidelines as agreed in advance with my supervisor and understand that I must comply with HYMS regulations and any other applicable code of ethics at all times.

Signature of Principal Investigator

Date: 27.05.2022

Print Name: Dr Laura Fitton

Signature of Student Investigator

Date: 27.05.2022

Print Name: Miss Lauren Spencer

SECTION A - CHECKLIST OF ENCLOSURES

(ETHICS TRAINING)

Study Plan / Protocol	See section C2
Recruitment advertisement	N/A
Participant information sheet	X
Participant Consent form	X
Research Participant Advocate Consent form	N/A
Evidence of external approvals	N/A
Questionnaires on sensitive topics	N/A
Interview schedule	X
Debriefing material	N/A
Other (please specify):	N/A
Evidence of peer review (If section H1 = Yes)	X
Draft NRES Form (for studies that require NRES approval and/or University Sponsorship)	N/A
Will this research be compliant with General Data Protection Regulation 2018? – Yes or No	Yes
Have the researchers completed mandatory research ethics and integrity training (University of Hull Staff only)? – Yes/No or N/A	N/A

SECTION B - IDENTIFYING INFORMATION

B1) Title of the research (PLEASE INCLUDE A SHORT LAY TITLE IN BRACKETS).

Anterior dental loading and the role of neck musculature during masticatory and para-masticatory activities

B2) Principal Investigator ☐ OR Supervisor X (please check as appropriate)

Title:	Dr	**Staff number:**	033155
Forename/Initials:	Laura C	**Surname:**	Fitton
Post:	Senior Lecturer in Anatomy	**Department:**	Hull York Medical School
Telephone:	01904321791	**E-mail:**	laura.fitton@hyms.ac.uk

B3) Co-applicants (including student investigators)

Title and Name	Post / Current programme (if student investigator)	Department/ School/Institution if not HYMS	Phone	Email
Miss Lauren Spencer	MPhil in Archaeology	Department of Archaeology at University of York	07860600605	ls2012@york.ac.uk

B4) Address for Correspondence

PalaeoHub University of York Wentworth Way Heslington York

SECTION C - PROJECT DETAILS

C1) Proposed study dates and duration (RESEARCH **MUST NOT BEGIN** UNTIL ETHICAL APPROVAL HAS BEEN OBTAINED)

Please complete as appropriate:

EITHER

a) Starting as soon as ethical approval has been obtained X (please check if applicable)

Approximate end date:	September 2022

OR

b) Approximate dates:

Start date:	09/03/23	**End date**:	09/03/23

C2) Give a full lay summary of the purpose, design and methodology of the planned research.

Background to planned Research

A prominent feature of Neanderthal skulls is their robust-looking skull and face shape that has been theorised to have evolved to deal with high mechanical forces from heavy use of their anterior teeth, this is known as the anterior dental loading hypothesis. Recent studies have explored this hypothesis using computer modelling known as Finite Element Analysis (FEA), which allow the user to investigate the stress and strain environments experienced by bone and teeth during mechanical loading. Surprisingly these studies have found minimal differences between modern humans and Neanderthals in their ability to sustain anterior dental loads. However, loadings used in FEA models of the skull, for both human clinical, evolutionary, and developmental research, are always significantly simplified, and maybe leading to inaccurate results. Neck musculature activation during certain feeding and para-masticatory behaviours are never included and could dramatically alter stress and strain environment within the skull during biting tasks. This study plans to create a finite element model of a modern human skull to investigate whether the inclusion of neck muscle forces during different biting behaviours could impact craniofacial stress and strain. If their inclusion has a significant impact then future FE models should consider including them. The role of these muscles during different bites could also shed light on the unique craniofacial form of Neanderthals.

Methodology for Research

1) **Creation of a FEA model of a human skull** – Using a CT scan of a modern human skull (taken from the New Mexico Decedent Image Database (NMDID) https://nmdid.unm.edu/) a cranium will be virtually segmented to create a 3D virtual model and converted into a finite element model (using FEA software VoX-FE). Using several human full head MRI scans, which have been previously collected by Dr Fitton (Previous HYMS ethical approval REF: 20 18 - June 2020) neck musculature and the muscles of mastication origin and insertions, and cross-sectional areas will be estimated. These estimates will be used to help create the boundary conditions and loadings for the FEA model.

2) **Collection of muscle activation data –** In order to see if neck muscles are activated during masticatory and para masticatory feeding behaviours muscle activation data will be collected (*in vivo*) on 1-5 healthy volunteers (already recruited as part of the study previously mentioned) using non-invasive surface electromyography (EMG).

EMG measures muscle response, or electrical activity in response to a nerve's stimulation of the muscle. During the test, surface electrodes sensors (conductive adhesive pads) will be placed on the skin above the relevant muscles on the head and neck; masseter and temporalis (muscles of mastication) and various neck muscles (semispinalis capitis, splenius capitis, sternocleido-mastoid, and trapezius). These electrodes are non-invasive and no pain or stimulation should be felt. The electrical activity picked up by the electrodes is then displayed on a computer monitor which displays electrical activity in the form of waves. We will measure the electrical activity of the muscles during rest, slight contraction and forceful contraction during different tasks. Muscle tissue does not normally produce electrical signals during rest.

The tasks participants will then be asked to carry out different masticatory and para-masticatory behaviours: 1) vertical bites on each tooth onto a piezoelectric bite force transducer at different gapes, 2) anterior tooth clench on a piece of fabric, 3) anterior tooth clench and simultaneous pull on a piece of fabric, 4) anterior tooth clench and simultaneous pull on a piece of fabric, whilst scraping the fabric with a blunt flint, 5) normal feeding on each tooth on a tough food item (chewy sweet and plant based jerky), 6) normal feeding on each tooth on a hard food item (carrot and apple).

Bite force (N) will be recorded for the participant at each tooth using the piezoelectric bite force transducer. Whilst the actions are being recorded, a 3D surface scanner (an Artec Eva– ideally designed for face scanning) will be used to record head position, so this positional data can be included in the FEA model. Photos will also be taken as a record of the experimental set up.

3) **Use of this data to load the FEA model** - The muscle activation data collected from the EMG testing will then be input into a series of finite element analysis (FEA) models of a human skull (each simulating a biting task carried out by the participant). The FEA models are virtual computer models (originally developed for the field of engineering to predict how various structure will respond to load). Given different boundary and loading conditions (muscle activations and constraints) it is expected that different stresses and strains will be produced for different tasks. If neck musculature is not important then its inclusion in the FEA models during head extension takes will have no impact on skull stress and strain. However, if there is a significant difference then neck musculature is likely needed to be included in future for accurate modelling.

C3) List any research assistants, sub-contractors or other staff not named above who will be involved in the research and detail their involvement.

N/A

C4) List below all research sites, and their Lead Investigators, to be included in this study.

Research Site	Individual Responsible	Position and contact details
PalaeoHub, University of York	Dr Laura Fitton	Principal investigator Email: laura.fitton@hyms.ac.uk
PalaeoHub, University of York	Dr Phil Cox	Head of the Paleohub, where the bite force, EMG and modelling work will take place. Email: philip.cox@hyms.ac.uk

C5) Are the results of the study to be disseminated in the public domain?

YES ☒ NO ☐

- ***If not, why not?***

n/a

C6) **Give details of the funding of the research, including funding organisation(s), amount applied for or secured, duration, and institutional reference**

Funding Body	Amount	Duration	UoH Reference
Self funded	N/A	N/A	N/A

C7) **Give details of any interests, commercial or otherwise, you or your co-applicants have in the funding body.**

N/A

SECTION D - EXPEDITED REVIEW

D1)

	Yes/No
a) Will the study involve recruitment of participants outside the UK?	No
b) Does the study involve participants who are particularly vulnerable or unable to give informed consent? *(e.g. children, people with learning or communication disabilities, people in custody, people engaged in illegal activities such as drug-taking, your own students in an educational capacity) (Note: this does not include secondary data authorised for release by the data collector for research purposes.)*	No
c) Will the study require obtaining consent from a "research participant advocate" (for definition see guidance notes) in lieu of participants who are unable to give informed consent? *(e.g. for research involving children or, people with learning or communication disabilities)*	No
d) Will it be necessary for participants, whose consent to participate in the study will be required, to take part without their knowledge at the time? *(e.g. covert observation using photography or video recording)*	No
e) Does the study involve deliberately misleading the participants?	No
f) Will the study require discussion of sensitive topics that may cause distress or embarrassment to the participant or potential risk of disclosure to the researcher of criminal activity or child protection issues? *(e.g. sexual activity, criminal activity)*	No
g) Are drugs, placebos or other substances (e.g. food substances, vitamins) to be administered to the study participants or will the study involve invasive, intrusive or potentially harmful procedures of any kind?	Yes
h) Will samples (e.g. blood, DNA, tissue) be obtained from participants?	No
i) Is pain or more than mild discomfort likely to result from the study?	No
j) Could the study induce psychological stress or anxiety or cause harm or negative consequences beyond the risks encountered in normal life?	No
k) Will the study involve prolonged or repetitive testing?	No
l) Will financial inducements (other than reasonable expenses and compensation for time) be offered to participants?	No
m) Will the research be conducted overseas and if so, has the appropriate local approvals been sought?	No

D2)

	Yes/No
a) Will the study seek written, informed consent?	Yes
b) Will participants be informed that their participation is voluntary?	Yes
c) Will participants be informed that they are free to withdraw at any time?	Yes
d) Will participants be informed of aspects relevant to their continued participation in the study?	Yes
e) Will participants' data remain confidential?	Yes
f) Will participants be debriefed?	Yes

If you have answered 'no' to all items in SECTION D1 and 'yes' to all questions in SECTION D2 the application will be processed through expedited review.

If you have answered "Yes" to one or more questions in Section D1, or "No" to one or more questions in Section D2, but wish to apply for expedited review, please make the case below. See research ethics website for an example "case for expedited review". ***If overseas approval is required, please provide confirmation that this has been obtained.***

D3) **Case for Expedited Review –** *To be used if asking for expedited review despite answering YES to questions in D1 or NO to answers in D2.*

D1g was designated as 'yes' due to the use of food and non-food items during biting tasks which will be placed in the mouth, and in the case of the food items may be swallowed.

The participant will be asked to bite down on a bite force transducer as well as on various food items (plant-based jerky, chewy sweets, apple and carrot) and non-food items (rope, fabric) while kinematic and muscle data are being recorded. None of these items are harmful or toxic.

The food items will all be plant-based to allow for a wider pool of potential candidates (vegans and vegetarians). All of the non-food items will be made of food safe materials (rope and fabric). The participant will be made aware of the food items to be consumed before consenting to the experiments.

A questionnaire (see attached) will also be provided to the participant ahead of their inclusion into the study to check for allergies to any of these materials.

SECTION E - PARTICIPANT DETAILS

E1) How many participants will be recruited?

1-5

E2) How was the number of participants decided upon?

The average/most suitable EMG data recorded from the participants will be used in the FEA model. We need at least one individual to collect data from but will collect data from up to five participants if time allows.

E3)

a) Describe how potential participants in the study will be identified, approached and recruited.

Three participants have already been identified as part of a previous study run by Dr Laura Fitton and Mr Thomas Baird (Previous HYMS ethical approval REF: 20 18, June 2020).

However, if one of the identified candidates drops out, or is no longer meets the inclusion criteria, additional CAHS staff, PhD students and MSc students from the Human Anatomy and Evolution and Clinical Anatomy PGT courses will be invited to participate. CAHS run weekly research meetings where students and staff present current work. I plan on presenting my research proposal to the group. If anyone meets the selection criteria and is interested in participating then I would recruit them. HYMS staff will also be sent a recruitment email if others are not interested (see attached).

b) Inclusion criteria:

The participant must be an adult with a full set of teeth, with no other orthodontic interventional in the past 5 years. If more than five participants apply, they will be filtered depending on their similarity to the individual used in the CT scan from NMDID for the FEA model (morphology, age, sex), if after that there are still more than 5 potential participants, they will be dealt with in the order in which they apply.

c) **Exclusion criteria:**

Any individual who does not meet the inclusion criteria will be excluded.

d) **Are any specific groups to be excluded from this study? If so please list them and explain why:**

None

e) **Give details for cases and controls separately if appropriate:**

N/A

f) **Give details of any advertisements:**

N/A

E4)

a) **State the numbers of participants from any of the following vulnerable groups and justify their inclusion**

Children under 16 years of age:	None
Adults with learning disabilities:	None
Adults with dementia:	None
Prisoners:	None
Young Offenders:	None
Adults who are unable to consent for themselves:	None
Those who could be considered to have a particularly dependent relationship with the investigator, e.g. those in care homes, students of the PI or Co-applicants:	Students of the supervisor will not be excluded from consideration. However, it will be made clear to them (verbally by Dr Fitton) that there is no need/expectation for them to participate. We see no conflict of interest. If they meet the criteria and would like to participate this will be an exciting opportunity for them to learn more about masticatory biomechanics.
Other vulnerable groups (please list):	None

b) **State the numbers of healthy volunteer participants:**

Healthy Volunteers	1-5

E5)

a) **Describe the arrangements for gaining informed consent from the research participants.**

All potential participants will be provided with an information sheet and consent form. Additionally, the student investigator will explain the purpose of the project and any potential risks of participation verbally.

b) **If participants are to be recruited from any of the potentially vulnerable groups listed above, give details of extra steps taken to assure their protection,**

including arrangements to obtain consent from a legal, political or other appropriate representative in addition to the consent of the participant *(e.g. HM Prison Service for research with young offenders, Head Teachers for research with children etc.).*

No additional arrangements are planned.

c) **If participants might not adequately understand verbal explanations or written information given in English, describe the arrangements for those participants (e.g. translation, use of interpreters etc.)**

N/A

d) **Where informed consent is not to be obtained (including the deception of participants) please explain why.**

N/A

E6) What is the potential for benefit to research participants, if any?

The research participant will benefit from the knowledge of their own contribution to human evolutionary anatomy and craniofacial maxillary research. They will also learn about EMG and get experience of experimental *in vivo* working environments.

E7) State any fees, reimbursements for time and inconvenience, or other forms of compensation that individual research participants may receive. Include direct payments, reimbursement of expenses or any other benefits of taking part in the research?

Refreshments will be provided, and any reasonable travel costs will be reimbursed.

SECTION F - RISKS AND THEIR MANAGEMENT

F1) Describe in detail the potential physical or psychological adverse effects, risks or hazards (minimal, moderate, high or severe) of involvement in the research for research participants.

EMG data collection requires close skin contact for measurement, requiring contact sites to be clean shaven. This has potential issues for abrasion and skin damage. Contacts pads are held to the skin with a mild adhesive, to ensure no adverse reaction a patch test will be performed before the procedure.

Bite force readings will be measured using a bite force transducer and participants asked to bite on some hard and tough food items and fabric. As such there is a very small chance of tooth fracture, albeit this would be the same risk the participant would experience during normal feeding and pulling on fabric with the teeth. Participants will be told not to attempt anything beyond their normal oral capabilities. Participants will be referred to a dental practitioner should any dental complication arise following the experiment and costs covered.

The scraping on hide tasks require participants scrape towards their hand with a blunt item resulting in a minimal risk of hitting themselves with the blunt item.

There is a possible risk of choking/gagging due to inhalation of food items (although no more risky than present during normal eating). To mitigate the risk of choking/gagging during the experiment we will first ensure that the participant has control over the placement of the food and non-food items within their mouth, secondly a trained safety officer will be informed and ready when the procedure takes place.

F2) Explain how the potential benefits of the research outweigh any risks to the participants.

Understanding how the skull loads during feeding and non-masticatory behaviours is of significant interest to craniofacial surgeons, dentists, anatomical scientists and anthropologists. Accurate loading is essential to predict bone modelling and remodelling events but the way FE models are currently being build is oversimplified and lacking in a group of muscles (the neck musculature) which could have a significant impact on skull loading. By participating in this study the participants will help collect vital data needed to create a realistic FE model. This model will not only shed light on the evolutionary history of our own species but can be used to understand craniofacial variability and masticatory pathologies.

F3) Describe in detail the potential adverse effects, risks or hazards (minimal, moderate, high or severe) of involvement in the research for the researchers.

Contact with the participants saliva is likely, therefore protective masks (3-ply surgical face mask), hypoallergenic gloves and protective eyewear will be worn throughout the procedure.

F4) Will individual or group interviews/questionnaires discuss any topics or issues that might be sensitive, embarrassing or upsetting, or is it possible that criminal or other disclosures requiring action could take place during the study (e.g. during interviews/group discussions, or use of screening tests for drugs)?

YES ☐ NO X

- ***If Yes, give details of procedures in place to deal with these issues.***

N/A

F5) Describe the measures in place in the event of any unexpected outcomes or adverse events to participants arising from their involvement in the project

General risk assessment forms will be completed and the safety officer responsible for the site alerted prior to the start of the procedure. First aiders will be on site (Becky Knight).

F6) Explain how the conduct of the project will be monitored to ensure that it conforms with the study plan and relevant University policies and guidance.

The project is subject to a Dissertation Advisory Panel (DAP), consisting of Dr Emily Hunter and supervisor Dr Laura Fitton. Current study plan has been approved by the lead

Research Project supervisor, Dr Emily Hunter. The lead investigator (Lauren spencer) also has weekly meetings with his supervisor, Dr Laura Fitton, to discuss the project.

SECTION G - DATA ACCESS AND STORAGE

G1) Where the research involves any of the following activities at any stage (including identification of potential research participants), state what measures have been put in place to ensure confidentiality of personal data (e.g. encryption or other anonymisation procedures will be used)

Electronic transfer of data by magnetic or optical media, e-mail or computer networks	All data, such as virtual models and video taken of the participant, will be anonymised and stored on the HYMS secure drive. No data will be transferred via email.
Sharing of data with other organisations	N/A
Export of data outside the European Union	N/A
Use of personal addresses, postcodes, faxes, e-mails or telephone numbers	Anonymization procedures will be used.
Publication of direct quotations from respondents	Anonymization procedures will be used.
Publication of data that might allow identification of individuals	Digital video will be taken of the participant undergoing chewing, any publication of images taken from such video would be processed to ensure anonymity
Use of audio/visual recording devices	Digital video cameras will be used to take videos of the participant during mastication. Videos will be deleted off the cameras memory after being stored on a secure server.
Storage of personal data on any of the following:	
Manual files	N/A
Home or other personal computers	N/A
University computers	Any digital data (FEA model) will be stored on the HYMS secure drive. Files will be named in such a way as to aid easy identification of the type of data stored within, and will include numbering which corresponds to a lab book which will also be stored digitally.
Private company computers	N/A

Laptop computers	Electromyography will require the use of a facility laptop containing relevant software for recording of EMG data. The laptop will not leave the PalaeoHub building and any data on the laptop will be deleted once uploaded to a secure server.

G2) Who will have control of and act as the custodian for the data generated by the study?

Dr Laura Fitton

G3) Who will have access to the data generated by the study?

Miss Lauren Spencer, Dr Laura Fitton, and Mr Thomas Baird

G4) For how long will data from the study be stored?

Anonymised data, models and simulations produced during the study will be retained by Dr Laura Fitton for future research and publication indefinitely. If the participant decides to withdraw from the study partway through, they will be given the option as to whether their data is stored, maintained, and used for the remainder of the study.

SECTION H – PEER REVIEW

H1)

a) **Has the project undergone peer review?**

YES X NO ☐

b) ***If yes, by whom was this carried out?*** *(please enclose evidence if available)*

This project has been approved by the DAP panel (Dr Emily Hunter and Dr Laura Fitton), 21st April 2022.

Participant Information Sheet

Study Title:

Anterior dental loading and the role of neck musculature during masticatory and para-masticatory activities

Invitation to Participate

We would like to invite you to take part in a research project. It is important that you understand the purpose of this study and what it will involve before you decide whether you would like to participate. Please read this information sheet carefully and discuss with others if you wish. If you would like more information, or there is something you do not understand, please contact the research team. There are no negative consequences should you choose to not participate.

What is the purpose of the study?

During feeding, muscles contract and food is broken down between teeth. During this process the skull is exposed to internal forces and deformed (resulting in stresses and strains). It is known that bone models, remodels and thus adapts in response to such mechanical loading, so understanding how the skull is loaded during different biting tasks could shed light on why our skull has developed and evolved into the form it has.

This study will collect muscle activation patterns from the neck and face of human participants during various feeding and biting tasks. Muscle activation will be recorded via surface electromyography (EMG) with non-invasive, painless, adhesive pads stuck onto the participant's skin. The data recorded will then be used to simulate mechanical loading in a computer model (finite element analysis) of a modern human skull. Different loadings recorded from the participant will be applied to the model and stress/strain comparisons made.

If significant differences in muscle activation patters are found between biting tasks, we aim to investigate which loading condition the human skull appears most mechanically adapted to. We also aim to see how inaccurate finite element results could be due to errors in muscle modelling. Currently such models only include the jaw muscles but it is here proposed that neck musculature could have a significant role in biting tasks.

HULL YORK MEDICAL SCHOOL

Why have I been chosen to take part?

We need five healthy adult volunteers to conduct biting tasks whist EMG data is being recorded. It is important that you have not undergone any orthodontic treatment in the last 5 years and are currently not experiencing issues with oral health.

Do I have to take part?

No. It is up to you to decide whether or not to take part. If you do, you will be given this information sheet to keep, and asked to complete a questionnaire. You will be given the opportunity to speak to the investigators and once you agree to participate you will be asked to sign a consent form. If you feel uncomfortable about any aspect of the study, please let the researcher know straight away. You are free to withdraw any time and without giving a reason. If you decide to withdraw, please tell the researcher.

What will happen if I take part?

If you would like to participate we will invite you to attend a meeting with the investigators at the Palaeohub, University of York. The researchers here will be happy to further explain the project for you, outline any risks, and give you an opportunity to ask any questions. At your convenience a trained researcher in masticatory biomechanics and dental anatomy will check with you that you have all the required teeth, and ask you to complete a questionnaire about your oral health and dental history, i.e. what orthodontic/dental treatment you may have had. There will be a few questions on your general diet (i.e. vegan, vegetarian, etc.), this information is required but will not affect whether you are selected. We will also ask you to do a patch test to check for allergies to the surface electrodes. These electrodes are non-invasive, and EMG is a common procedure that will not cause any harm or pain. If you experience irritation from the patch test unfortunately you will not be able to participate further in the study. This pre-test will take about 1 hour.

If you meet the selection criteria we will arrange for you to return again for a day of data collection. During this day EMG surface electrodes will be placed on your neck and face. Muscle data will be collected from your neck and jaw muscles whilst you are undertaking various biting behaviours. During these tasks jaw movements will be recorded using a surface scanner and video.

You will be asked to bite on some hard and tough food and non-food items, as well as a bite force transducer (a plastic covered sensor that measures bite force). You will also be asked to grip some material between your teeth and pull forward/scrape on the object. You will not be asked to bite at any force beyond your normal capabilities.

Once the electrodes have been placed on your face and neck they need to remain in place until all the data has been collected. The full day (9.30am-4pm) will be split up into data collection and rest periods to avoid any fatigue. Lunch and snacks during breaks will be provided. The experiment can, and will stop, at any time you request.

Will you compensate me for my time?

Refreshments will be available to all participants.

Are there any advantages in taking part?

You will help to contribute to more accurate musculoskeletal modelling by helping us understand how the skull loads during masticatory and non-masticatory behaviours. This can be used by craniofacial surgeons, dentists, anatomical scientists and anthropologists to create more realistic FEA models to predict bone modelling and remodelling events which could have a significant impact on skull loading.

Are there any other disadvantages or risks in taking part?

In taking the EMG readings the contact points will be connected to the skin via small adhesive pad. The adhesive in the electrode contact points is very mild and can be removed very easily, to ensure no reaction takes place a patch test, where a sample of the adhesive is applied in an inconspicuous area will be undertaken first. Contact sites will need to be clean shaven/exfoliated to attach the contacts, a razor, shaving foam and exfoliating pads will be provided for you.

When bite force readings are taken you will be asked to bite down on some tough and hard food items and some non-food items such as a force transducer, you should not exceed your normal bite strength as this can lead to tooth damage such as chipping.

What if I am unhappy or if there is a problem?

If you have a concern about any aspect of this study, you should ask to speak with the researchers who will do their best to answer your questions. They may be reached using the contact details given at the end of this sheet. If you remain unhappy and wish to complain formally, please contact the HYMS Research Office via research@hyms.ac.uk or 01482 461918 or 01482 464723.

On what basis will you process my data?

Under the General Data Protection Regulation (GDPR), the University has to identify a legal basis for processing personal data and, where appropriate, an additional condition for processing special category data.

In line with our charter which states that we advance learning and knowledge by teaching and research, the University processes personal data for research purposes under Article 6 (1) (e) of the GDPR:

Processing is necessary for the performance of a task carried out in the public interest.

Special category data is processed under Article 9 (2) (j):

Processing is necessary for archiving purposes in the public interest, or scientific and historical research purposes or statistical purposes.

Research will only be undertaken where ethical approval has been obtained, where there is a clear public interest and where appropriate safeguards have been put in place to protect data.

In line with ethical expectations and in order to comply with common law duty of confidentiality, we will seek your consent to participate where appropriate. This consent will not, however, be our legal basis for processing your data under the GDPR.

What will happen to my information?

Appropriate technical and organisational precautions will be taken to ensure that any personal data that you share is kept safe. Your name and details will not be associated with the data collected, and only the minimum amount of data necessary for the project will be collected. In addition, all data will be anonymised and identified only using an anonymised participant identifier. Digital data will be stored on encrypted and password protected computers in a secure facility. Contact details for participants will only be known by the principal investigator, Lauren Spencer, and project supervisor Dr Laura Fitton.

All of your data will be anonymised. Video recordings taken during the procedure will be stored in a secure server, any images published will be anonymised.

Scan images and models constructed from these images will be included in the published study. Your name will not be included in any published material, and you will never be named directly in any of our findings. If you would like to receive a summary of the research findings, we will send you one once the study is completed.

If you are happy for us to do so, we would like to archive data following the project, so it is available to others for future research. Data would be anonymised and would not identify you. We will not store data however, if you do not want us to.

Has this project received ethical approval?

Yes

Who is organising and funding the research?

The study is being organised by Lauren Spencer, MPhil student, under supervision of Dr Laura Fitton. This research is self-funded.

What happens next?

If you are interested in taking part or would like more information please contact:

Lauren Spencer, MPhil Student, University of York

Email: ls2012@york.ac.uk

Phone: 07860 600 605

Or

Dr Laura Fitton, Senior Lecturer in Anatomy

Email: laura.fitton@hyms.ac.uk

If you are chosen for the study you will be contacted by email

Thank you for taking the time to read this information sheet.

Consent Form

Title of Study:

Anterior dental loading and the role of neck musculature during masticatory and para-masticatory activities

Student Researcher Miss Lauren Spencer

Supervisor Dr Laura Fitton

If you wish to participate in this study, please initial the appropriate responses and sign and date the declaration at the end of this document.

	Initials
• I have read the participant information sheet and had the opportunity to ask questions. I understand the answers provided and know what taking part in the study will involve.	☐
• I understand that participation is voluntary, and I am free to withdraw at any time. Any data collected. I do not have to give a reason, and this will not affect my future academic or employment status.	☐
• I understand that the procedure being carried out has some minor risk associated with it and that I may experience some mild discomfort during the procedure.	☐
• I understand that if I withdraw from the study, I will be given the option as to whether the data already collected will be allowed to be maintained and used for the purposes of this study.	☐
• I understand that the information I supply will be confidential and will not be shared with others **unless** circumstances arise that breach safeguarding practices (e.g. if myself or others are at risk of harm).	☐
• I understand that the information I provide may be published and this may include direct quotations. Pseudonyms will be used (a name that is not my own) however, to protect my identity.	☐
• I understand that images of my teeth, 3D facial models, and stills from video taken during the experiment may be included in any publication arising from this research. These images will be anonymised.	☐
• I agree to my anonymised data being stored following the project so that it is available indefinitely to others for future research.	☐
• I understand that this is not a diagnostic service and that no clinical advice will be offered	☐
• I have completed a dietary/allergies/oral health questionnaire	☐
• I understand that I will be asked to consume food items and place foreign materials between my teeth.	☐
• I agree to participate in this research project.	☐

Name of Participant	Date	Signature
……………………………………………	………….…………	………..………………………..
Name of Person taking consent	Date	Signature
……………………………………………	………….…………	………..………………………..

When completed, 1 copy for participant; 1 for researcher