

**Biomechanical consequences of variation in shoulder morphology
in the Hominoidea**

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BIBLIOGRAPHISCHE DARSTELLUNG

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Dissertation

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Studies of comparative morphology clearly distinguish the shoulder morphology of *Homo* from that of the other hominoids. While the shoulder morphology of non-human hominoids is thought to signal adaptations to arboreal locomotion, human shoulder morphology is understood to have lost this adaptation during hominin evolution. Ideas how non-human hominoid shoulder morphology is advantageous in an arboreal context suggest that the specific shoulder morphological traits enhance the arm-raising mechanism. However, this idea has not been biomechanically tested. This thesis constitutes the first analysis of the biomechanical consequences of two distinct shoulder morphologies within Hominoidea by comparing the glenohumeral muscle capabilities of *Gorilla* to *Homo*. The biomechanical capabilities are evaluated by constructing a computational musculoskeletal model of a gorilla thorax, shoulder girdle and upper arm, which is used to predict relevant biomechanical metrics such as muscle moments and moment arms. Muscle moments and moment arms are predicted for two important mechanisms, arm-raising and arm-lowering. The predictions are compared to those of an already existing human musculoskeletal model in order to evaluate differences in arm-raising and arm-lowering capability based on the two distinct thorax and shoulder girdle morphologies. The results of the biomechanical analyses show that the arm-lowering mechanism is enhanced in *Gorilla* compared to *Homo*, instead of the arm-raising mechanism. The enhanced arm-lowering mechanism is evident by greater moment capacities of two important arm-lowering muscles, pectoralis major and teres major. The greater moments are the result of greater muscle force capacities and greater moment arms, due to the beneficial musculoskeletal geometry of *Gorilla*. The results highlight that a more distal muscle insertion along the humerus has the greatest enhancing effect on the arm-lowering moment arms of teres major and pectoralis major. Furthermore, thorax and shoulder girdle morphological traits that are well known to distinguish non-human apes from humans were found to contribute to the enhancement of the arm-lowering mechanism. The more cranially oriented glenoid, obliquely oriented scapular spine and cranial scapula position on the thorax enabled certain muscles to act as arm-lowering muscles in *Gorilla*, contrary to the arm-raising action capability that is predicted for *Homo*. The enhanced arm-lowering capability is likely advantageous for the arboreal locomotion of apes. During hoisting behaviours that are known to occur during suspension and vertical climbing, arm-lowering is used to lift the heavy body of the apes upward. The results of this thesis in conjunction with earlier EMG studies suggest those muscles which are highly activated during these hoisting behaviours also have enhanced arm-lowering capacities in *Gorilla* and potentially other non-human hominoids compared to *Homo*. As such, the results highlight shoulder morphological traits that are biomechanically important for the arboreal locomotor behaviour of apes. By this, the thesis demonstrates a link between the conformation of shoulder morphological traits and their biomechanical capability, which will aid future functional interpretations of extant and extinct species.

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SUMMARY

INTRODUCTION

Shoulder morphology displays a high variability within primates. Many studies demonstrate that similar scapular shapes are exhibited by primate species employing similar locomotor types, despite different degrees of phylogenetic relationship (Miller, 1932; Inman *et al.*, 1944; Ashton and Oxnard, 1964; Roberts, 1974; Larson, 1993; Larson, 1995; Young, 2008; Schmidt and Krause, 2011; Arias-Martorell *et al.*, 2015; Young *et al.*, 2015). Therefore, shoulder morphology is understood to exhibit a functional signal for specific locomotor behaviours across primates. However, the mechanical advantages of specific shoulder morphologies for primate locomotor behaviours are still poorly understood.

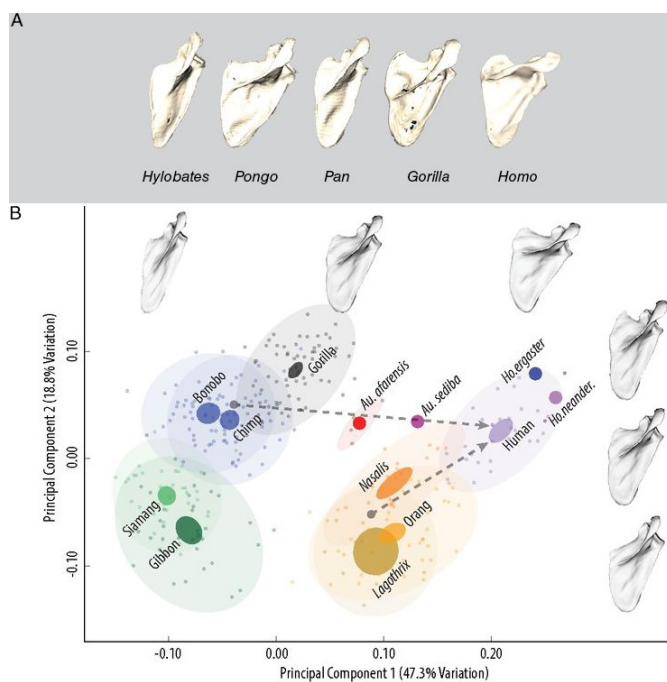


Figure 1 Scapula shape variation of extant and extinct primates, after Young *et al.* (2015). A. Scapula shape variation within Hominoidea. B. Results of principal component analysis. PC1 describes orientation of the spine and glenoid relative to the vertebral border of the blade whereas PC2 describes differences in the borders of the supraspinous fossa.

Within the Hominoidea, studies of comparative morphology demonstrated that the scapula of humans is well distinguished from the scapulae of the non-human apes (Miller, 1932; Ashton and Oxnard, 1964; Oxnard, 1967; Young, 2008; Young *et al.*, 2015). Furthermore, the scapular morphology of non-human apes covaries with that of suspensory monkeys. This covariation of scapular morphology was understood as evidence for convergent evolutionary adaptations to similar arboreal locomotor modes. The morphological traits shared by suspensory monkeys and arboreal apes, which separate them from humans, are a more obliquely oriented scapular spine and a cranially oriented acromion that projects well beyond a cranially oriented glenoid (Figure 1). Those traits were thought to signal adaptation to suspensory locomotion.

In the past, researchers have differently phrased ideas as to how the aforementioned morphological traits are advantageous in an arboreal context. A prominent proposal, which relates to the need for highly elevated arms during suspensory locomotion, suggests that the scapular morphology shared by non-human apes and suspensory monkeys enhances the arm-raising mechanism (Larson, 1993). In particular, the action of the deltoid muscle, the main arm-raising muscle in humans, was thought

to be enhanced, both through a greater mechanical advantage provided by the cranially oriented glenoid and through a greater leverage provided by the greater acromion projection and scapular spine orientation (Miller, 1932; Roberts, 1974; Corruccini and Ciochon, 1976; Ciochon and Corruccini, 1977). However, this proposal has not been biomechanically tested.

In recent years, behavioural studies of apes have further complicated the functional interpretation of scapular morphology. Non-human apes have traditionally been classified as a group of suspensory species. However, the frequency of arboreal locomotor behaviour within this group is highly diverse. Gorillas, despite exhibiting a scapular morphology characterised as suspensory (Figure 1, left side of PC1), rarely employ forelimb suspension as adults (Doran, 1997; Taylor, 1997; Remis, 1998; Crompton *et al.*, 2010; Crompton, 2016). This divergence between morphological signal and locomotor frequency, described as the “gorilla paradox” (Remis, 1998), has led to uncertainties regarding functional interpretations based on scapular shapes within apes. This uncertainty is amplified by the fact that we still have a poor understanding of the biomechanical consequences of different shoulder morphologies.

AIM OF THESIS

This thesis constitutes the first biomechanical evaluation of the consequences of different shoulder morphologies observed within the Hominoidea. By this evaluation, the thesis aims to overcome the current gap between morphological observations and functional interpretations. The objectives are as follows:

1. Enhance understanding of biomechanical consequences of shoulder morphology in the Hominoidea.
2. Evaluate earlier ideas proposing an enhancement of the arm-raising mechanism in arboreal hominoids.
3. Investigate functional consequences of differences in shoulder musculoskeletal geometry for the glenohumeral muscles.
4. Determine differences of biomechanical capabilities between the *Gorilla* and *Homo* musculoskeletal shoulder system.

The biomechanical analyses constitute comparisons of the capabilities between *Gorilla*, a species that exhibits the typical ‘suspensory’ scapular morphology, and *Homo*, which lacks these scapular traits. The capabilities are compared by estimating muscle moments and moment arms of the glenohumeral muscles of both species. These biomechanical metrics relate to colloquial terms like enhanced leverage or mechanical advantage (Sherman *et al.*, 2013). Moment is the product of muscle force and muscle moment arm and an indicator for the “wellness” of a musculoskeletal system (Michilsens *et al.*, 2010). While muscle force is dependent on soft tissue properties, moment arm is defined as the perpendicular (or minimal) distance between muscle line of action and joint rotation centre. The metric is dependent on the orientation of the joint centre relative to the muscle attachment points. Therefore, moment arm is a measure of the mechanical properties of the musculoskeletal geometry.

In comparison, greater moment arms would indicate greater biomechanical capability that is enhanced by musculoskeletal geometry. Greater moments would demonstrate greater biomechanical capability due to enhanced musculoskeletal properties (soft and hard tissue).

OVERVIEW OF RESULTS

Overview of Results

This cumulative dissertation consists of two first-authored peer-reviewed papers. Chapter 1 was published in the *Journal of Anatomy* (van Beesel *et al.*, 2021) and Chapter 2 was published in the *American Journal of Biological Anthropology* (van Beesel *et al.*, 2022).

Chapter 1. Exploring the functional morphology of the *Gorilla* shoulder through musculoskeletal modelling

The functional morphology of the *Gorilla* shoulder was studied by developing a specimen-specific musculoskeletal model of a female western lowland gorilla (*Gorilla gorilla*). This musculoskeletal model is a computational representation of the shoulder morphology of the specimen that allows the computation of muscle moments and moment arms for different tasks. The model includes the main shoulder bones as well as the ribcage and hip, and the main glenohumeral arm-raising muscles, the deltoid, supraspinatus and infraspinatus. The morphology and soft-tissue property data to develop the model were collected during a dissection using a combination of different imaging techniques.

Earlier proposals suggested that non-human ape scapular morphology enhances the arm-raising mechanism compared to humans. These proposals were evaluated by comparing muscle moment arm and moment estimates during arm-raising of the newly developed gorilla shoulder model to those of a human model previously published by Seth *et al.* (2019). The estimates were used to assess the biomechanical effectiveness of the arm-raising mechanism in both species.

The results of the biomechanical assessment suggest that the arm-raising capability is similar in gorillas and humans. This is evident through comparable muscle moment arm and moment values across arm-raising in both species. This similarity in arm-raising capability indicates that non-human ape scapular morphology does not provide an advantageous configuration for the arm-raising mechanism, contrary to earlier ideas. However, gorilla-specific muscle force-length properties facilitate the maintenance of a greater arm-raising moment capacity when the arm is in an overhead position. This high arm-raising capacity at greater arm elevation angles might benefit the arm-raising and holding in highly elevated positions in *Gorilla* compared to *Homo*.

The lack of a signal for an enhanced arm-raising mechanism of the deltoid, the main arm-raising muscle, is especially surprising. The moment arm of the acromial deltoid, the middle part of the muscle, is similar in *Gorilla* and *Homo* (Figure 2). The similarity suggests that the greater lateral acromion projection and more cranial oriented glenoid of non-human apes do not provide a biomechanical enhancement or greater leverage for this muscle, contrary to earlier suggestions. Furthermore, the spinal deltoid (posterior part) that acts as an arm-raising muscle in humans displays an arm-lowering action capability, evident by a negative moment arm, in the gorilla (Figure 2). This difference in action capability is the result of a caudal shift of the muscle line of action relative to the joint rotation centre, which is caused by the more oblique oriented scapular spine and the cranially oriented glenoid. These results suggest that the cranially oriented scapular spine and glenoid shared by non-human apes and humans cause an enhancement of the arm-lowering rather than an arm-raising mechanism.

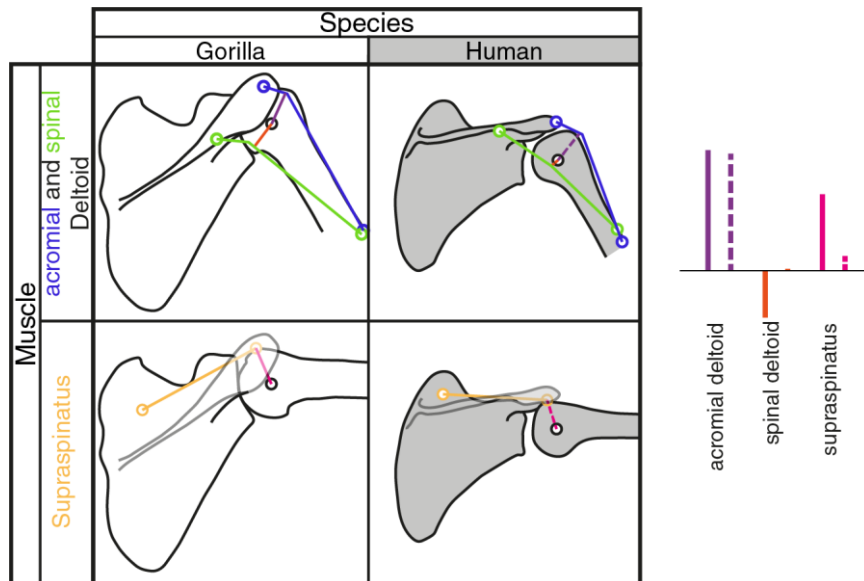


Figure 2 Biomechanical consequences of shoulder morphology for the glenohumeral arm-raising muscles. Left side: Each moment arm estimate is depicted as a line connecting the glenohumeral joint centre (black circle) and the muscle line of action (different coloured bands). Right side: Moment arm bar plots of the respective muscles of the gorilla (solid) and human (dashed) at the depicted arm positions (left side). Upward-facing bars indicate arm-raising, downward-facing bars indicate arm-lowering action capability.

The biomechanical assessment further highlights a remarkable difference in the supraspinatus arm-raising capability between gorillas and humans. The arm-raising capability is enhanced in *Gorilla*, which is evident by greater muscle moment arms and moments compared to *Homo*. However, the greater moment arm is caused by a more lateral projecting greater tubercle on the humeral head in *Gorilla* (Figure 2), not by differences in scapular morphology. The greater supraspinatus force-producing capacities, which are the result of a more massive muscle size, and the greater moment arm lead to the greater moment capacity in *Gorilla* compared to *Homo*. The results highlight that humerus morphology, rather than scapular morphology, has a stronger effect on supraspinatus arm-raising capability in the two species.

In conclusion, the results do not support the earlier hypothesis that non-human ape scapular morphology enhances the arm-raising mechanism compared to humans.

Chapter 2. Comparison of the arm-lowering performance between *Gorilla* and *Homo* through musculoskeletal modeling

The results of chapter one showed that *Gorilla*-specific scapular morphology does not enhance the arm-raising mechanism compared to *Homo*. Instead, the shift to an arm-lowering action capability of the spinal deltoid suggests that the obliquely oriented scapular spine and cranially oriented glenoid, earlier understood as arboreal scapular traits of non-human hominoids, are beneficial for the arm-lowering mechanism. In order to investigate whether gorilla scapular morphology enhances the arm-lowering mechanism compared to humans, the previously developed gorilla musculoskeletal model was extended by adding important arm-lowering muscles. The arm-lowering capacity estimates between the gorilla model and the previously described human model (Seth *et al.*, 2019) were compared to investigate the effects of scapular morphology on the arm-lowering mechanism.

The results of the biomechanical analysis highlight that arm-lowering is enhanced in *Gorilla* compared to *Homo*. The enhanced arm-lowering mechanism is evident by greater (more negative) moment arm and moment capacities for two important arm-lowering muscles, pectoralis major and

teres major (Figure 3). The greater moment-generating capacity is the result of the greater moment arms and greater maximum isometric force-producing capabilities in *Gorilla* compared to *Homo*. The differences in moment arm and moment-producing capacities greatly exceed those observed for the arm-raising muscles (compare Figures 2 and 3).

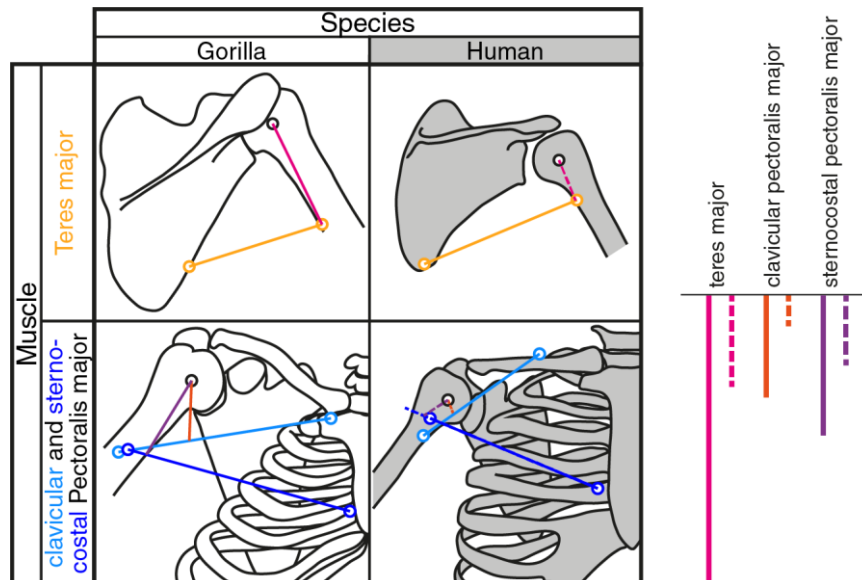


Figure 3 Biomechanical consequences of shoulder morphology for the glenohumeral arm-lowering muscles. Left side: Each moment arm estimate is depicted as a line connecting the glenohumeral joint centre (black circle) and the muscle line of action (different coloured bands). Right side: Arm-lowering moment arm bar plots of the respective muscles of the gorilla (solid) and human (dashed) at the depicted arm positions (left side). The downward-facing bars indicate an arm-lowering capability.

The greater moment arms in *Gorilla* are evidence for a biomechanical enhancement based on differences in shoulder musculoskeletal geometry. The modelling results indicate that the skeletal trait mainly responsible for enhancing the arm-lowering mechanism is humerus morphology and muscle insertion location. In *Gorilla*, teres major and pectoralis major were found to insert further distally on the humerus compared to humans (Figure 3). This more distal location extends the distance between muscle line of action and glenohumeral joint centre and thereby enhances the muscle moment arm.

Scapular musculoskeletal geometry has a lesser, though still notable, effect on teres major and pectoralis major moment arms. In teres major, the cranially oriented glenoid results in a cranial position of the glenohumeral joint centre relative to the muscle insertion site, compared to the lateral joint centre position in humans (Figure 3, first row). This difference causes a greater distance between the joint centre and muscle path and a further-enhanced arm-lowering moment arm. In the clavicular portion of pectoralis major, the cranial glenoid orientation, cranial position of the scapula on the thorax and a muscle origin that is concentrated on the manubrium enhance the moment arm of this muscle unit (Figure 3, second row). However, the gorilla thorax and shoulder girdle morphology of *Gorilla* is not beneficial to the arm-lowering capability of sternocostal pectoralis major.

In conclusion, the results highlight that the *Gorilla* arm-lowering mechanism is enhanced through beneficial morphological traits and greater force capacities compared to *Homo*.

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ZUSAMMENFASSUNG

EINLEITUNG

Die Schultermorphologie innerhalb der Primaten zeichnet sich durch eine hohe Variabilität aus. Viele wissenschaftliche Arbeiten, die diese Variabilität dokumentierten, demonstrierten, dass ähnliche Scapula-Formen bei Primatenarten auftreten, die ebenfalls ähnliche Fortbewegungsarten nutzen, unabhängig vom Verwandtschaftsgrad (Miller, 1932; Inman *et al.*, 1944; Ashton and Oxnard, 1964; Roberts, 1974; Larson, 1993; Larson, 1995; Young, 2008; Schmidt and Krause, 2011; Arias-Martorell *et al.*, 2015; Young *et al.*, 2015). Demzufolge stellt Schultermorphologie ein funktionelles Signal für bestimmte Fortbewegungsarten innerhalb der Primaten dar. Allerdings bleiben die biomechanischen Konsequenzen der unterschiedlichen Schultermorphologien für das Fortbewegungsverhalten der Primaten ungeklärt.

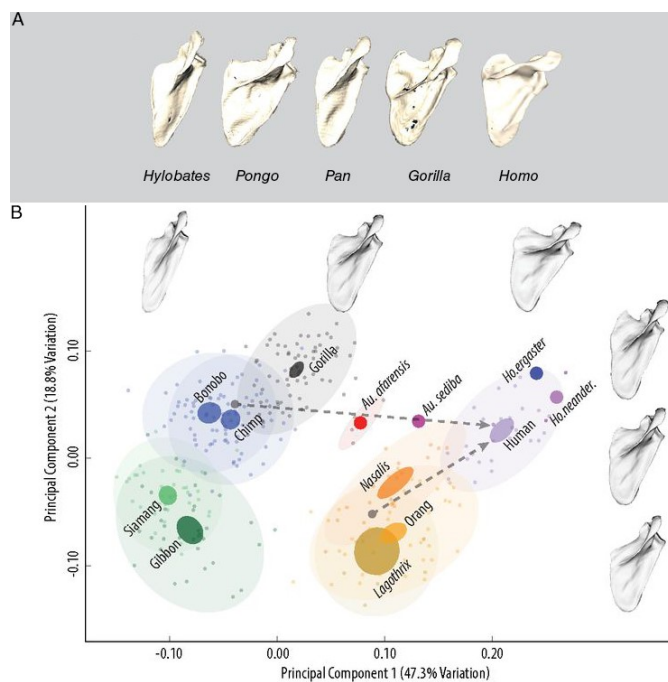


Abbildung 1 Variation von Scapula-Formen rezent und extinkter Primaten, nach Young *et al.* (2015). A. Variation von Scapula-Formen innerhalb der Hominoidea. B. Ergebnisse einer Hauptkomponentenanalyse. PC1 beschreibt die Orientierung der Spina scapulae und der Fossa glenoidea relativ zum vertebralen Rand wohingegen PC2 die Unterschiede in den Grenzen der Fossa supraspinata beschreibt.

Innerhalb der Hominoidea zeigten Studien, dass sich die Scapula von Menschen stark von der anderer Menschenaffen unterscheidet (Miller, 1932; Ashton and Oxnard, 1964; Oxnard, 1967; Young, 2008; Young *et al.*, 2015) (Abbildung 1 A). Des Weiteren kovariert die Scapula von Menschenaffen mit der von anderen sich suspensorisch fortbewegenden Primaten. Diese Kovariation von Scapulamorphologie gilt als Nachweis für die konvergente evolutionäre Anpassung an ähnliche arborikole Fortbewegungsweisen. Die morphologischen Merkmale, die von suspensorischen Affen und arborikolen Menschenaffen geteilt werden, und die sie von Menschen abgrenzen, sind: eine diagonal verlaufende Spina scapulae und ein kranial ausgerichtetes Acromion, welches deutlich über die kranial ausgerichtete Fossa glenoidea herausragt (Abbildung 1 B, entlang PC1). Diese Merkmale signalisieren, so wird vermutet, eine Anpassung an die suspensorische Fortbewegung.

In der Vergangenheit haben Wissenschaftler unterschiedliche Vermutungen darüber formuliert wie die zuvor beschriebenen morphologischen Merkmale einen Vorteil im arborikolen Lebensraum darstellen. Eine favorisierte Hypothese, welche sich auf die Notwendigkeit von ständig erhobenen Armen während hangelnder Fortbewegung bezieht, besagt, dass die Scapulamorphologie, die Menschenaffen und suspensorischen Affen gemeinsam ist, den Armhebemechanismus verstärkt. (Larson, 1993). Man vermutete, dass vor allem die Wirksamkeit des Deltoid Muskel, der primäre Armhebemuskel im Menschen, verstärkt sei, sowohl durch einen größeren mechanischen Vorteil aufgrund der kranial ausgerichteten Fossa glenoidalis als auch durch einen größeren Hebel, ermöglicht durch den großen Vorsprung des Acromions und der diagonalen Spina scapulae (Miller, 1932; Roberts, 1974; Corruccini and Ciochon, 1976; Ciochon and Corruccini, 1977). Diese Hypothese wurde bisher jedoch nicht biomechanisch getestet.

In den vergangenen Jahren haben Verhaltensbeobachtungen von Menschenaffen die funktionelle Interpretation der Scapulamorphologie weiter verkompliziert. Arborikole Menschenaffen wurden traditionell als eine Gruppe suspensorischer Arten klassifiziert. Allerdings unterscheidet sich die Häufigkeit von arborikolem Fortbewegungsverhalten innerhalb der Gruppe stark voneinander. Gorillas, obwohl sie die für hangelnde Fortbewegung charakteristische Scapulamorphologie aufweisen (Abbildung 1, linke Seite der PC1), bewegen sich als adulte Tiere selten hangelnd fort (Doran, 1997; Taylor, 1997; Remis, 1998; Crompton *et al.*, 2010; Crompton, 2016). Die Divergenz zwischen morphologischem Signal und Häufigkeit der Fortbewegung, genannt das Gorilla Paradox (Remis, 1998), hat zu Unsicherheiten in Bezug auf die funktionale Interpretation basierend auf Scapula-Formen innerhalb der Menschenaffen geführt. Diese Unsicherheit wird dadurch verstärkt, dass die biomechanischen Konsequenzen unterschiedlicher Schultermorphologien immer noch unklar sind.

ZIEL DER DOKTORARBEIT

Diese Doktorarbeit stellt die erste biomechanische Evaluation der Konsequenzen der unterschiedlichen Schultermorphologien innerhalb der Hominoidea dar. Durch diese Evaluation beabsichtigt die Arbeit die momentane Lücke zwischen morphologischen Beobachtungen und funktionaler Interpretation zu schließen. Die Ziele sind folgende:

1. Verbesserung des Verständnisses der biomechanischen Konsequenzen der Schultermorphologie innerhalb der Hominoidea.
2. Evaluation von Hypothesen, die eine Verstärkung des Armhebemechanismus bei arborikolen Hominoiden vermuten.
3. Untersuchung der funktionalen Konsequenzen für die Schultergelenkmuskeln aufgrund unterschiedlicher muskuloskeletaler Geometrien der Schulter.
4. Feststellung von Unterschieden in den biomechanischen Kapazitäten zwischen den muskuloskeletalen Schulterssystemen von *Gorilla* und *Homo*.

Die folgenden biomechanischen Analysen umfassen einen Vergleich zwischen den Kapazitäten von *Gorilla*, einer Art, die die typisch „suspensorische“ Scapulamorphologie aufweist, und *Homo*, einer Art der diese speziellen Scapula Merkmale fehlen. Der Vergleich der Kapazitäten erfolgt über die Auswertung der Muskelkraftmomente und Muskelkraftarme der Schultergelenkmuskeln beider Arten. Diese biomechanischen Messgrößen stellen einen Zusammenhang zu kolloquialen Begriffen wie „verstärkter Hebel“ oder „mechanischer Vorteil“ her (Sherman *et al.*, 2013). Kraftmoment ist das Produkt aus Muskelkraft und Muskelkraftarm und ein Indikator für die Kapazität eines muskuloskeletalen Systems (Michilsens *et al.*, 2010). Während Muskelkraft von den Eigenschaften des Weichgewebes abhängt, wird der Muskelkraftarm als der senkrechte (oder kleinste) Abstand zwischen der Wirkungslinie der Kraft und dem Rotationszentrum des Gelenks definiert. Aufgrund des-

sen ist der Kraftarm abhängig von der Orientierung des Gelenkzentrums relativ zu den Muskelsatzstellen. Der Muskelkraftarm ist dementsprechend ein Maß für die mechanischen Eigenschaften der muskuloskeletalen Geometrie.

Im Vergleich weisen größere Muskelkraftarme auf einen erhöhten muskulären mechanischen Vorteil hin, der verstärkt wird durch muskuloskeletale Geometrie. Größere Muskelkraftmomente dagegen demonstrieren höhere biomechanische Kapazitäten basierend auf verbesserten muskuloskeletalen Eigenschaften (Weich- und Hartgewebe).

ÜBERSICHT ÜBER DIE ERGEBNISSE

Diese kumulative Dissertation besteht aus zwei extern geprüften Erstautorpublikationen. Kapitel 1 wurde im *Journal of Anatomy* publiziert (van Beesel *et al.*, 2021) und Kapitel 2 wurde im *American Journal of Biological Anthropology* publiziert (van Beesel *et al.*, 2022).

Chapter 1. Exploring the functional morphology of the *Gorilla* shoulder through musculoskeletal modelling

Erforschung der funktionellen Morphologie der Gorilla Schulter durch muskuloskeletale Modellierung

Die funktionelle Morphologie der *Gorilla* Schulter wurde mit Hilfe der Entwicklung eines Subjekt-spezifischen muskuloskeletalen Modells eines weiblichen westlichen Flachlandgorillas (*Gorilla gorilla*) untersucht. Dieses muskuloskeletale Modell ist eine rechentechnische Repräsentation der Schultermorphologie eines Exemplars, welches es ermöglicht Muskelkraftmomente und –arme für unterschiedliche Tätigkeiten zu ermitteln. Das Modell beinhaltet die Schulterknochen sowie den Brustkorb und wichtige Armhebemuskeln des Schultergelenks; Deltoid, Supraspinatus und Infraspinatus. Die Daten über muskuloskeletale Morphologie und Eigenschaften der Weichgewebe, die für die Entwicklung des Modells benötigt werden, wurden während einer Sektion unter Verwendung verschiedenster bildgebender Verfahren gesammelt.

Bisherige Hypothesen besagen, dass die Scapulamorphologie nichtmenschlicher Hominoiden im Vergleich zu Menschen den Armhebemechanismus verstärkt. Hier wurden diese Hypothesen evaluiert indem die geschätzten Muskelkraftmomente und –arme während des Armhebens des neu entwickelten *Gorilla* Schultermodells mit denen eines Menschenmodells, zuvor publiziert von Seth *et al.* (2019), verglichen wurden. Die ermittelten Werte wurden benutzt um die biomechanische Effektivität des Armhebemechanismus beider Arten zu beurteilen.

Die Ergebnisse der biomechanischen Beurteilung deuten auf eine ähnliche Armhebekapazität bei Gorillas und Menschen hin. Dies wird deutlich durch vergleichbar große Muskelkraftmomente und –arme während des Armhebens bei beiden Arten. Diese Ähnlichkeit in der Armhebekapazität deutet an, dass die Scapulamorphologie, entgegen bisheriger Hypothesen, keine überlegene Konfiguration für den Armhebemechanismus darstellt. Allerdings fördern die *Gorilla*-spezifischen Kraft-Längen Eigenschaften der Muskel die Aufrechterhaltung höherer Armhebemomentkapazitäten, wenn sich der Arm in einer erhobenen Position befindet. Diese hohe Armhebekapazität bei größeren Armhebewinkeln könnte das Armheben und –halten in hoch erhobenen Positionen in *Gorilla* gegenüber *Homo* begünstigen.

Das Fehlen eines verbesserten Armhebemechanismus des Deltoid Muskels, des wichtigsten Armhebemuskels, ist besonders überraschend. Der Kraftarm des acromialen Deltoid, der mittlere Teil des Muskels, ist ähnlich in *Gorilla* und *Homo* (Abbildung 2). Die Ähnlichkeit deutet darauf hin, dass sowohl das weiter vorspringende Acromion sowie das kranial ausgerichtete Glenoid der nichtmenschlichen Hominoiden keine biomechanische Verbesserung und keinen größeren Hebel für diesen Muskel darstellen, entgegen bisheriger Annahmen. Des Weiteren agiert der spinodeltoideus

(posteriore Teil) als Armhebemuskel im Menschen. In Gorillas besitzt dieser Teil des Muskels allerdings eine Armsenkende Wirkungsfähigkeit, erkennbar an dem negativen Kraftarm (Abbildung 2). Dieser Unterschied in der Wirkungsfähigkeit ist das Resultat einer kaudalen Verschiebung der Wirkungslinie der Muskelkraft relativ zum Rotationszentrum des Gelenks, die hervorgerufen wird durch die diagonal ausgerichtete Spina scapulae und die kranial zeigende Fossa glenoidalis. Diese Ergebnisse deuten darauf hin, dass die kranial orientierten Spina scapulae und Fossa glenoidalis, die allen nicht-menschlichen Hominoiden und hangelnden Affen gemeinsam sind, den Armsenkungsmechanismus anstelle des Armhebemechanismus verstärken.

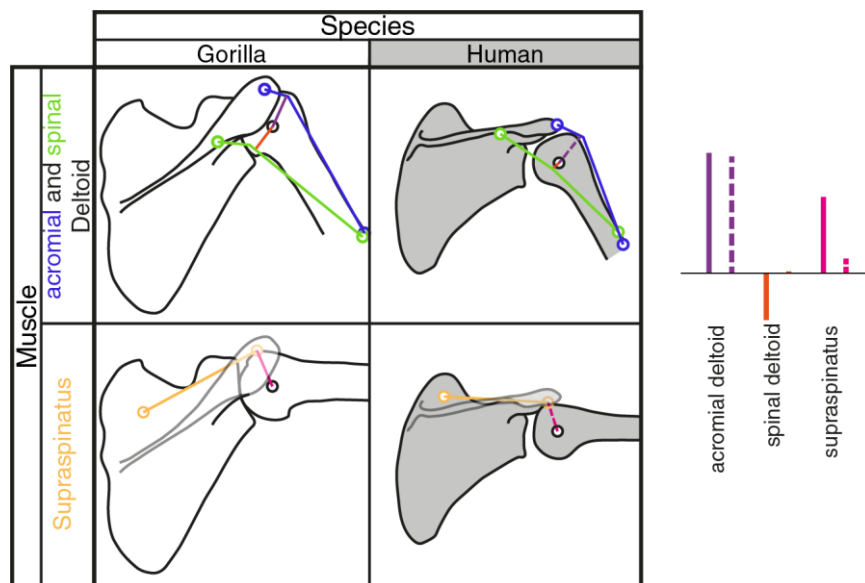


Abbildung 2 Biomechanische Konsequenzen der Schulter-Morphologie für die Armhebemuskeln des Schultergelenks. Linke Seite: Jede Kraftarmschätzung ist als Linie dargestellt, die das Zentrum des Schultergelenks (schwarzer Kreis) mit der Wirkungslinie des Muskels (unterschiedlich farbige Bänder) verbindet. Rechte Seite: Säulendiagramm der Kraftarme der jeweiligen Muskeln des Gorillas (durchgezogen) und Menschen (gestrichelt) in der gezeigten Armhaltung (siehe linke Seite). Kraftarme sind auf die Humeruslänge normalisiert. Die aufwärts zeigenden Säulen deuten auf eine Armhebende, die abwärts zeigenden Säulen auf eine Armsenkende Wirkungsweise hin.

Die biomechanische Beurteilung hebt zudem deutliche Unterschiede in der Armhebekapazität des Supraspinatus zwischen Gorillas und Menschen hervor. In *Gorilla* ist die Armhebekapazität, erkennbar an den höheren Muskelkraftmomenten und –armen, gegenüber *Homo* verstärkt. Die höheren Kraftarme werden jedoch von einem stärker lateral hervorstechenden großen Tuberculum des Humeruskopfes in *Gorilla* verursacht (Abbildung 2), nicht von den unterschiedlichen Scapulamorphologien. Die höheren Kräfte produzierenden Kapazitäten des Supraspinatus, welche das Resultat der verhältnismäßig größeren Muskelmasse sind, und die höheren Kraftarme führen zu der höheren Momentkapazität in *Gorilla* im Vergleich zu *Homo*. Die Ergebnisse weisen darauf hin, dass Humerusmorphologie anstatt Scapulamorphologie den größeren Effekt auf die Armhebekapazität des Supraspinatus in den beiden Arten hat.

Zusammenfassend stützen die Ergebnisse die bisherigen Hypothesen nicht, die einen stärkeren Armhebemechanismus bei nicht-menschlichen Hominoiden gegenüber Menschen aufgrund unterschiedlicher Scapulamorphologien vermuteten.

Chapter 2. Comparison of the arm-lowering performance between *Gorilla* and *Homo* through musculoskeletal modeling

Vergleich der Armsenkungsleistung zwischen *Gorilla* und *Homo* durch muskuloskeletale Modellierung

Die Ergebnisse von Kapitel eins haben gezeigt, dass die für *Gorilla* spezifische Scapulamorphologie den Armhebemechanismus im Vergleich zu *Homo* nicht verstärkt. Stattdessen deutet der Wechsel zu einer Armsenkungsfähigkeit des spinodeltoids darauf hin, dass die diagonal orientierte Spina scapulae und die kranial zeigende Fossa glenoidalis, ursprünglich definiert als Scapulamerkmale für die Anpassung an die hangelnde Fortbewegungsweise nicht-menschlicher Hominoiden, den Armsenkungsmechanismus begünstigen. Um zu untersuchen ob die *Gorilla* Scapulamorphologie den Armsenkungsmechanismus im Vergleich zu Menschen verstärkt, wurde das zuvor entwickelte muskuloskeletale Modell des Gorillas um wichtige Armsenkungsmuskeln erweitert. Die ermittelten Armsenkungskapazitäten des Gorillamodells und mit dem zuvor beschriebenen Menschenmodell (Seth *et al.*, 2019) verglichen um die Wirkung der Scapulamorphologie auf den Armsenkungsmechanismus zu untersuchen.

Die Ergebnisse der biomechanischen Analyse verdeutlichen, dass der Armsenkungsmechanismus in *Gorilla* im Vergleich zu *Homo* verstärkt ist. Der verstärkte Armsenkungsmechanismus ist ersichtlich aufgrund der höheren Kraftmomente und –arme zweier wichtiger Armsenkungsmuskeln, Teres major und Pectoralis major (Abbildung 3). Die höhere Momentkapazität in *Gorilla* ist das Resultat der verglichen mit *Homo* größeren Kraftarme und der Fähigkeit, größere isometrische Maximalkräfte zu produzieren. Die Unterschiede zwischen den Kraftmomenten und –armen übersteigen deutlich die Unterschiede, die zwischen den Armhebemuskeln der beiden Arten beobachtet wurden (vergleiche die Säulendiagramme in den Abbildungen 2 und 3).

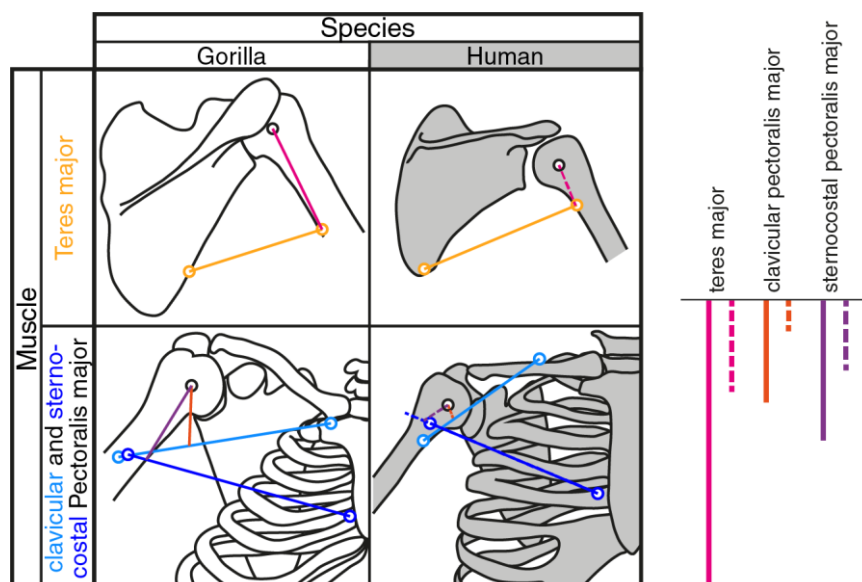


Abbildung 3 Biomechanische Konsequenzen der Schulter-Morphologie für die Armsenkungsmuskeln. Linke Seite: Jede Kraftarmschätzung ist als Linie dargestellt, die das Zentrum des Schultergelenks (schwarzer Kreis) mit der Wirkungslinie des Muskels (unterschiedlich farbige Bänder) verbindet. Rechte Seite: Säulendiagramm der Armsenkungskraftarme der jeweiligen Muskeln des Gorillas (durchgezogen) und Menschen (gestrichelt) in der gezeigten Arm-Haltung (siehe linke Seite). Kraftarme sind auf die Humeruslänge normalisiert. Die abwärts zeigenden Säulen deuten auf eine Armsenkende Wirkungsweise hin.

Die größeren Kraftarme von *Gorilla* sind Beweis für die biomechanische Verstärkung basierend auf den Unterschieden in der muskuloskeletalen Geometrie der Schulter. Die Ergebnisse der Modellierung zeigen, dass die Humerusmorphologie und die Position der Muskelansatzstellen hauptsächlich für den verstärkten Armsenkungsmechanismus verantwortlich sind. In *Gorilla* wurde festgestellt, dass die Muskeln Teres major und Pectoralis major weiter distal am Humerus ansetzen als in Menschen (Abbildung 3). Die distale Position erweitert die Distanz zwischen der Wirkungslinie der Muskeln und dem Zentrum des Schultergelenks und verstärkt dadurch den Kraftarm der Muskeln.

Die muskuloskeletale Geometrie der Scapula hat einen geringeren, jedoch immer noch relevanten Effekt auf den Kraftarm von Teres major und Pectoralis major. Im Fall von Teres major resultiert die kraniale Orientierung der Fossa glenoidea in einer kranialen Position des Schultergelenkzentrums relativ zum Muskelursprung, verglichen mit der lateralen Position des Gelenkzentrums in Menschen (Abbildung 3, erste Reihe). Dieser Unterschied sorgt für eine größere Distanz zwischen dem Gelenkszentrum und dem Muskelpfad und vergrößert so den Kraftarm. Im Falle des clavikulären Teils des Pectoralis major verstärken die kraniale Ausrichtung der Fossa glenoidea, die kraniale Position der Scapula auf dem Thorax und der Muskelursprung, der auf das Manubrium konzentriert ist, den Kraftarm dieser Muskeleinheit (Abbildung 3, zweite Reihe). Die Morphologie des Thorax und Schultergürtels stellt jedoch keinen Vorteil für die Armsenkungskapazität des sternocostalen Pectoralis major dar.

Zusammenfassend zeigen die Ergebnisse, dass morphologische Merkmale der Schulter und größere Kapazitäten der Muskelkraft von *Gorilla* gegenüber *Homo* einen Vorteil für den Armsenkungsmechanismus darstellen.

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Chapter 1

Exploring the functional morphology of the *Gorilla* shoulder through musculo-skeletal modelling

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Exploring the functional morphology of the *Gorilla* shoulder through musculoskeletal modelling

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Abstract

Musculoskeletal computer models allow us to quantitatively relate morphological features to biomechanical performance. In non-human apes, certain morphological features have long been linked to greater arm abduction potential and increased arm-raising performance, compared to humans. Here, we present the first musculoskeletal model of a western lowland gorilla shoulder to test some of these long-standing proposals. Estimates of moment arms and moments of the glenohumeral abductors (deltoid, supraspinatus and infraspinatus muscles) over arm abduction were conducted for the gorilla model and a previously published human shoulder model. Contrary to previous assumptions, we found that overall glenohumeral abduction potential is similar between *Gorilla* and *Homo*. However, gorillas differ by maintaining high abduction moment capacity with the arm raised above horizontal. This difference is linked to a disparity in soft tissue properties, indicating that scapular morphological features like a cranially oriented scapular spine and glenoid do not enhance the abductor function of the gorilla glenohumeral muscles. A functional enhancement due to differences in skeletal morphology was only demonstrated in the gorilla supraspinatus muscle. Contrary to earlier ideas linking a more obliquely oriented scapular spine to greater supraspinatus leverage, our results suggest that increased lateral projection of the greater tubercle of the humerus accounts for the greater biomechanical performance in *Gorilla*. This study enhances our understanding of the evolution of gorilla locomotion, as well as providing greater insight into the general interaction between anatomy, function and locomotor biomechanics.

KEYWORDS

3D modelling, adduction–abduction, hominoid shoulder, moment arms, musculoskeletal model, scapula functional morphology, western lowland gorilla

1 | INTRODUCTION

It is generally accepted that non-human apes possess adaptations to arboreal environments that are not shared by humans. While arboreal adaptations can be found throughout the ape skeleton, they

are thought to be particularly important in the shoulder. In relation to their orthograde body plan, hominoid shoulders sit more dorsally and further apart on the transversely broad thorax compared to quadrupedal monkeys and most quadrupedal mammals (Cartmill & Milton, 1977; Ward, 2007). This shift in position potentially allows

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for a wider range of upper limb motion, which enables the upright hand-assisted locomotion that most hominoids display in arboreal contexts. Apes further share a unique set of morphological features in the shoulder that are traditionally understood as reflecting adaptations to their arboreal environments.

Correlational studies of functional morphology have shown that primates sharing a given mode of locomotion also share a particular suite of morphological features in the shoulder. Non-human apes use vertical climbing and forelimb suspension to navigate arboreal habitats and share the following skeletal features: cranially divergent clavicles, a cranially oriented scapular spine, acromion and glenoid, a laterally projecting acromion, a superoinferiorly elongated blade, a medially positioned inferior angle and a relatively large supraspinous fossa (Ashton & Oxnard, 1964; Ciochon & Corruccini, 1977; Corruccini & Ciochon, 1976; Melillo, 2016; Miller, 1932; Oxnard, 1967; Roberts, 1974; Young, 2008). These same features occur in distantly related monkey species that are especially suspensory (Jenkins et al., 1978; Larson, 1995, 1998), but not in humans or other primarily terrestrial primates (Figure 1). This co-occurrence of form and function provides circumstantial evidence of adaptation to arboreality, especially given the commonality of convergence. Accordingly, studies from the late 19th through mid-20th centuries commonly characterized all non-human apes as brachiators.

However, there is a growing recognition that the shoulder form-function link is not as tight as once believed within apes (Larson, 2015; Larson & Stern, 2013; Melillo, 2016; Taylor, 1997). Gorillas are members of the superfamily Hominoidea and exhibit the shoulder features described above that are traditionally understood as adaptations to below-branch forelimb suspension. However, forelimb suspension is employed infrequently in adults. Arboreal postural behaviours for adult gorillas mostly consist of resting and feeding. The actual arboreal locomotion is confined to rare events of climbing in and out of food trees using vertical climbing and of traveling between feeding sites within trees by brachiating and orthograde clambering (Crompton et al., 2010). Juveniles between about 5 months and 2 years spend half or more of their time in trees,

exhibiting climbing and suspension behaviours. However, they become full quadrupedal knuckle-walkers after the age of four, when the relative frequency of arboreal locomotion declines to nearly zero (Doran, 1997). Furthermore, the relative amount of time spent in arboreal contexts differs between gorilla subspecies, with mountain gorillas spending substantially more time on the ground than lowland gorillas. Particularly, lowland gorillas display a 20% frequency of the locomotor modes vertical climbing and descent, compared to 1% in mountain gorillas (Crompton, 2016; Crompton et al., 2010). However, this difference in locomotor and positional behaviour is not reflected in bone morphology: these taxa exhibit little to no difference in scapular features linked to arboreal adaptation (Taylor, 1997). Thus, *Gorilla* is no longer recognized as an especially suspensory genus, despite exhibiting the characteristic morphology of the suspensory shoulder and forearm—a circumstance that has been labelled the gorilla paradox (Remis, 1998).

Shoulder morphology reflects a complicated interplay of functional signal and phylogenetic inertia in apes. The confounded functional and phylogenetic division in this group makes it difficult to separate morphological features indicating arboreal adaptation from features that simply reflect membership in the Hominoidea. Enhancing our understanding of the biomechanical benefits of ape shoulder morphology to arboreality is crucial for better disentangling these compound signals.

1.1 | Previous proposals

Researchers have proposed a number of ideas on how ape shoulder morphology could be biomechanically beneficial in an arboreal context. Despite the knowledge that multiple shoulder functions play a role during suspension (like propulsion and stabilization), ideas discussing how shoulder morphology is advantageous have focused on the specific action of arm-raising (see Larson, 1993 and references therein). The focus lies on arm-raising because all arboreal postural behaviours, including vertical climbing and forelimb suspension,

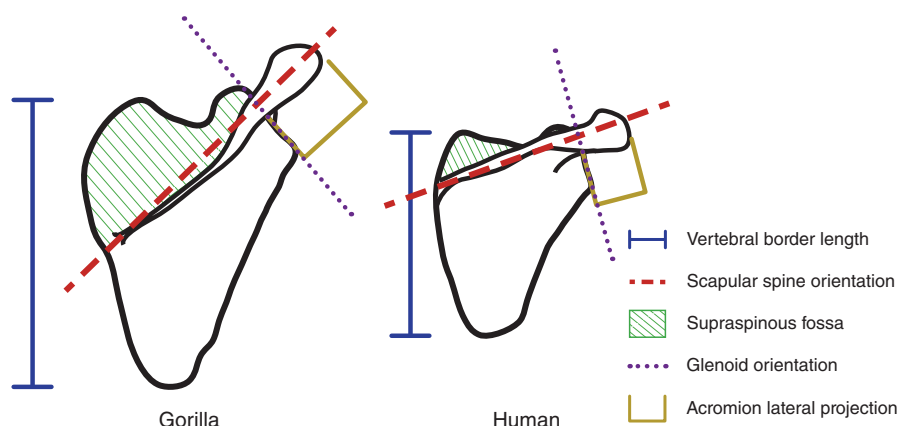


FIGURE 1 Differences in scapular morphology between gorillas and humans. The superoinferiorly elongated blade (along vertebral border), cranially oriented scapular spine, increased size of the supraspinous fossa, cranial orientation of glenoid and lateral projection of the acromion are understood as signals for suspensory adaptation in gorilla, and their absence in human as a signal for the loss of this adaptation

require the habitual use of the arm in an over-head position (Ashton & Oxnard, 1964). Furthermore, in gorillas and other non-human apes, powerful arm raising may be especially important due to their unique body plan. Their upper limbs are long (especially the forearm and hand) and heavy relative to overall body mass (Zihlman, 1992). Because a greater mass is located in distal segments, a larger inertial load must be overcome to raise the arm. The idea that arm-raising is an especially important mechanism during brachiation is further supported by the highly influential findings of Ashton and Oxnard (1964). Their results indicated that the main skeletal differences between brachiators and non-brachiators are related to the functional muscle group responsible for arm elevation. Moreover, Ashton and Oxnard (1963) found that these muscles are relatively more powerful in brachiators than in quadrupedal primates. Thus, apes may be expected to display adaptations that relate to a strong arm-raising mechanism.

In humans, arm-raising occurs by the combined movements of scapulothoracic rotation and glenohumeral elevation, a mechanism also referred to as scapulohumeral rhythm (Codman, 1934; Inman et al., 1944; Lucas, 1973). The muscles that function as scapular rotators, most importantly trapezius and serratus anterior, originate from the vertebral column and the ribs, and insert onto the scapular spine and medial border through the inferior angle. The main glenohumeral abductors, the deltoid and supraspinatus muscles, originate from the clavicle, scapular spine, acromion and supraspinous fossa and insert onto the deltoid tuberosity and greater tubercle of the humerus. Because the scapula serves as the primary anchor for muscles involved in arm raising, functional morphologists have focused on explaining how scapula shape affects the function of the glenohumeral abductors and scapular rotators.

However, proposed explanations are vague and sometimes contradictory. Miller (1932) suggested that the cranial orientation of the scapular spine aids the arm-raising mechanism by providing advantageous attachment locations to the glenohumeral abductors. Roberts (1974) similarly emphasized that the cranially "swept" acromion of non-human apes improves leverage for the deltoid muscle. Corruccini and Ciochon (1976) suggested that the lateral projection of the acromion, which was reported to be greater in *Gorilla* than in *Homo* (Ciochon & Corruccini, 1977), serves as a beneficial biomechanical arrangement for deltoid and trapezius muscles. In contrast, Ashton and Oxnard (1964) proposed that a cranially oriented scapular spine and elongated scapular blade enhance the function of the scapular rotators, rather than the glenohumeral abductors. This commonly cited explanation implies that the scapular rotation mechanism is expected to be more mechanically advantageous in non-human apes than it is in humans. However, there are indications that scapula rotation either does not occur during arm-raising in non-human apes (Tuttle & Basmajian, 1977) or that the mechanism differs from that documented in humans (Larson et al., 1991). Tuttle and Basmajian (1977) measured muscle activity of the cranial trapezius and caudal serratus anterior, which are thought to be the most important scapular rotators in humans, but found little to no activity in non-human apes during arm elevation. They concluded

that, due to a more cranially oriented glenoid, the scapula already faces cranially, similar to the fully rotated scapula in humans, and therefore apes would have less need for an active scapular rotation mechanism. In contrast, Larson et al. (1991) conducted similar experiments and found that caudal serratus was active during arm-raising motions. Therefore, Larson et al. proposed that caudal elongation and narrowing of the blade enhance serratus anterior leverage and thereby improve the scapular rotation mechanism (Larson, 2015; Larson et al., 1991), while spine orientation instead reflects an improved shoulder stabilization role of infraspinatus or a structural reinforcement of the scapular blade (Larson & Stern, 2013). However, none of these proposals have been biomechanically tested to date.

Testing these proposals has been challenging for various reasons. Generally, precisely measuring biomechanical parameters that relate to improved leverage or muscle mechanical efficiency is difficult in living animals, and requires invasive methods like marker-based radiography (An et al., 1984). To avoid these methodological issues, measurements are often taken from cadavers (An et al., 1984; Michilsens et al., 2010). However, as biomechanical properties such as leverage may be dependent on joint angles, the measurements have to be taken for different joint configurations and therefore the methods are often difficult and time-consuming (Channon et al., 2010; Murray et al., 1995). Furthermore, strong ethical restrictions apply to working with living apes and cadavers are difficult to acquire. Therefore, new methods were favoured to measure biomechanical parameters for locomotion patterns in non-human apes. Recent advances in the construction and analysis of musculoskeletal computer models provide such new opportunities to study biomechanical structures and relate their function to advantages in biomechanical performance (Seth et al., 2018).

1.2 | Musculoskeletal Modelling

Musculoskeletal models can be used to calculate the biomechanical properties that relate to enhanced muscle function, like moment and moment arm (Seth et al., 2018). These models are computer-based, often three-dimensional, representations of the musculoskeletal system that offer a way to understand performance capability. The models are grounded in mechanics as well as anatomy, thereby building upon the traditional approach of comparative functional morphology. Furthermore, the interactive virtual modelling approach permits the isolation of specific aspects of skeletal geometry or muscle properties to discern their impact on joint mechanics, without the involvement of live animals (Brassey et al., 2017; Hutchinson et al., 2005, 2015).

The total amount of rotational force produced about a joint (moment) is the result of the force produced by a muscle-tendon unit (MTU) during activation, multiplied by its moment arm. Musculoskeletal models include information about the architectural properties of MTUs and musculoskeletal geometry. Architectural properties like physiological cross-sectional area, fiber length, pennation angle and tendon slack length determine the force

production capability of a MTU (Delp et al., 2007; Delp & Loan, 2000; Hutchinson et al., 2015), whereas musculoskeletal geometry (i.e., muscle origin, insertion and path) affects a MTU's line of action and thus its distance from the joint rotation centre. The latter parameters determine moment arm, which quantifies how efficiently the linear force produced during muscular contraction is converted to moment. In this way, moment arm provides a measure of colloquial terms like (bio)mechanical advantage and leverage (Sherman et al., 2013). As moment combines effects of properties internal to a MTU with its external geometry, the parameter can be used as a measure of the functional capacity of a musculoskeletal system. Furthermore, the sign of moment arm, and consequently also of moment, indicates whether a muscle would act to increase or decrease joint angles and thus approximately predicts the function (e.g. abductor/adductor) of a muscle (Pandy, 1999), although there are important complexities in this prediction (Kuo, 2001). Because moment arms are strongly influenced by bone shape, size and (musculo)skeletal configuration, this parameter can provide insight into how aspects of skeletal morphology serve to alter forces generated by soft tissues.

In this study, we test the hypothesis that the musculoskeletal configuration of the shoulder in gorillas improves the biomechanical performance of the glenohumeral abductors over arm abduction, compared to humans. We investigate these issues by comparing moment arm and moment production potential of the deltoid, supraspinatus and infraspinatus between musculoskeletal models of the gorilla and human glenohumeral joints. We expect to find higher moment production capabilities in the gorilla model, reflecting an arm-raising mechanism that is stronger than in humans. We further expect that the osteological features discussed above (cranially divergent clavicles, cranially oriented scapular spine and laterally projecting acromion, etc.) will increase abductor moment arms. Higher moments correlated with higher moment arms would support previous ideas linking differences in skeletal morphology to functional enhancement, and thus the general inference that these features are adaptations to arm-raising.

2 | MATERIALS AND METHODS

The gorilla musculoskeletal model was built for use in the open-source software OpenSim (Delp et al., 2007; Seth et al., 2018). We also used OpenSim to make alterations to an existing human model (Seth et al., 2016, 2019) and to analyse the muscle moment arms and moment capacities of both models that are possible during glenohumeral abduction. The gorilla musculoskeletal model was informed by specimen-specific data (Figure 2), which was collected during a dissection that took place in April 2019. The skeletal input derived from a three-dimensional reconstruction of a CT-scan. Rotational degrees of freedom were measured on the cadaver during passive manipulation of the glenohumeral joint, to limit the range of motion of the virtual joint in the model. MTU geometry (attachment sites and paths) was reconstructed by three-dimensional surface scans

taken before and after muscles were removed. The MTU parameters informing the MTU's force properties were measured, calculated and estimated from data collected during the dissection.

2.1 | Components of a musculoskeletal model

Musculoskeletal models in OpenSim are based on three primary components: rigid bodies, joints and forces. Rigid bodies contain representations of individual bones or of articulated sets of bones. A three-dimensional anatomical coordinate system (ACS) is applied to each body, providing a framework to describe the position and orientation of bones, muscles and joints. Moreover, the rigid bodies are hierarchically structured. Bodies situated lower in the hierarchy (child bodies) sit within the coordinate system of bodies situated higher in the hierarchy (parent bodies). Joints define the possible movement of a child body relative to its parent. Each joint is composed of a joint-specific coordinate system (JCS), of coordinates that restrict the joint excursion (up to three rotational and three translational degrees of freedom) and of functions that define the movement path. Forces are able to control the movement of rigid bodies around the connecting joints and are informed by the geometry and properties of each MTU. The geometry is composed of a MTU's origin and insertion points and of a MTU's path, which is constrained by path points and wrapping surfaces. The parameters fibre length, pennation angle, physiological cross-sectional area and tendon slack length are used to scale the generic Hill-type muscles (Delp & Loan, 2000; Zajac, 1989). Because the goal of this study is to compare a human and a gorilla model, care was taken to build our gorilla model in a manner that maximizes comparability with the existing human model (Seth et al., 2016, 2019).

2.2 | Data acquisition

All observations informing the model came from the same female western lowland gorilla (*Gorilla gorilla*). The gorilla was a zoo animal, euthanized at 48.8 years (December 2012) after suffering from age-related ailments (heart failure and kidney problems). The dead mass was 80.5 kg. The fresh-frozen cadaver (stored at -20°C) was acquired ethically through collaboration with the Cleveland Museum of Natural History, Erie Zoo and Cleveland Metroparks Zoo. Data collection procedures and muscle property calculations are based on Hutchinson et al. (2015), with minor modification.

2.3 | Rigid body configuration

The specimen was CT scanned at the Ohio State University College of Veterinary Medicine using a Revolution Evo Lightspeed CT (GE Healthcare), prior to dissection. The scan (voltage: 120 kV; current: 319 mA) contained 1843 slices (voxel size: $0.977 \times 0.977 \times 0.625$ mm). Bones of the upper limb and thorax were manually segmented in

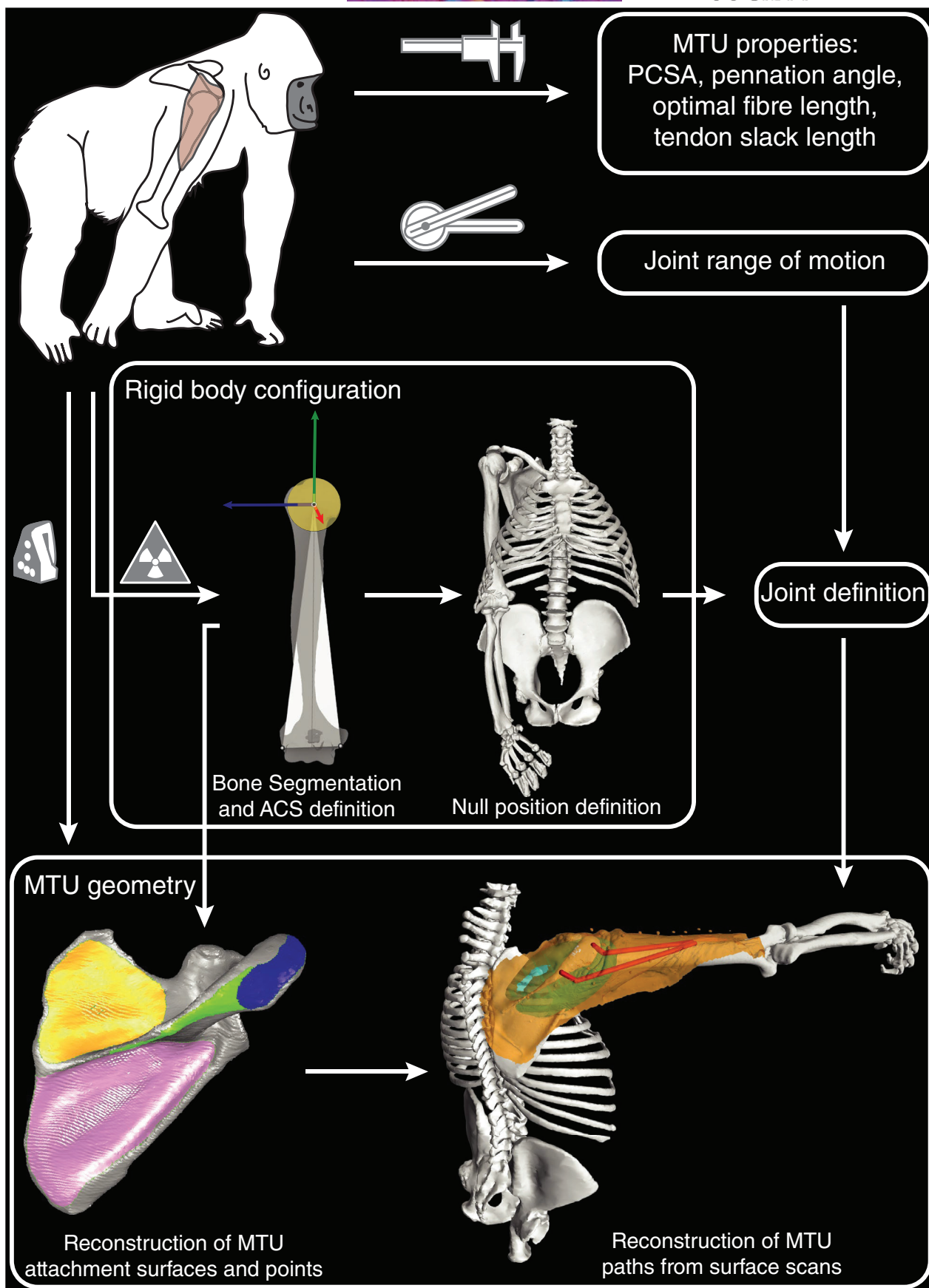


FIGURE 2 Organisational workflow of data acquisition and model construction. ACS, anatomical coordinate system; MTU, muscle-tendon unit; PCSA, physiological cross-sectional area

Avizo software (version 9.3.0, Visualization Sciences Group), using a thresholding approach. Meshes were decimated and smoothed in Geomagic Studio® (version 2013, RSI 3D-Systems). The model is composed of four rigid bodies: thorax (represented as a single body), clavicle, scapula and humerus (Figure 3). Meshes of the lower arm (radius, ulna and hand) are included for visualization purposes only.

ACSs were defined for thorax, clavicle, scapula and humerus in Rhinoceros software (version 6, McNeel Europe). Coordinate centre and orientation of axes are based on specific landmarks as described in the ISB recommendations (Wu et al., 2005; also see Seth et al., 2019). Following the recommendations, a sphere was used to define the centre of the humerus ACS (Figure 2) in a geometrically defined and semi-automatic manner via Matlab code (Bishop et al., 2020). The meshes with defined ACSs were next transferred into Maya software (version 2019, Autodesk), where the meshes were arranged hierarchically and the null position was defined (with humerus long axis in parallel to sagittal plane). These inputs were written into an OpenSim musculoskeletal model file using a Matlab script (Bishop et al., 2020). Rigid body hierarchy, ACS definitions and null positions are identical between gorilla and human models.

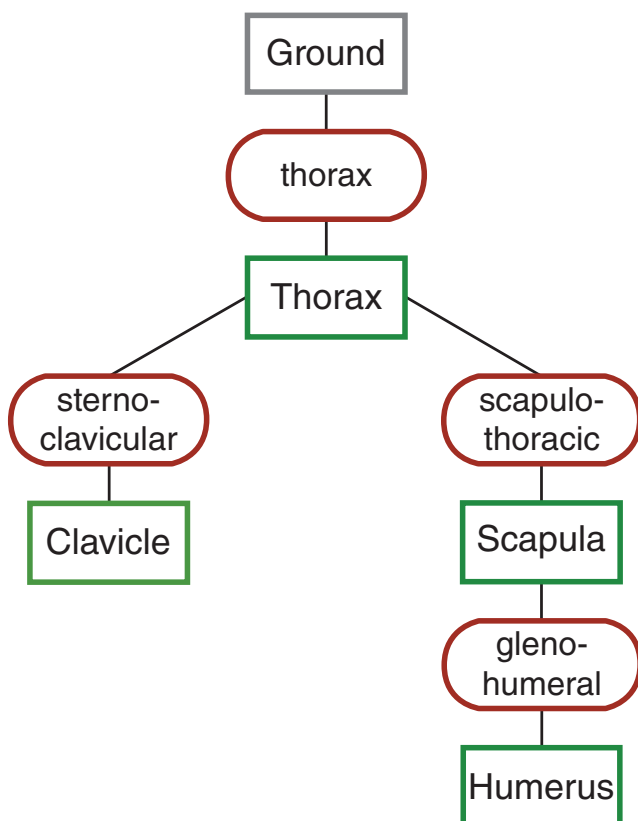


FIGURE 3 Composition of our gorilla musculoskeletal shoulder model. In the hierarchical chain of the model, joint names are lowercased in red circles, rigid body names are capitalized in green boxes. The hierarchy follows from top to bottom, with each child rigid body sitting below its parent rigid body. The rigid bodies Thorax, Clavicle and Scapula are held immobile in our analysis

2.4 | Joint definition

The shoulder complex consists of four different joints that describe the movement of the rigid bodies against each other (Figure 3). Their setup follows the ISB recommendations (Wu et al., 2005). In this study, analyses were carried out with all rigid bodies except the humerus kept immobile. In this way, we investigate performance of the glenohumeral joint while controlling for potential interspecific differences in scapulothoracic rotation during arm elevation. As recommended by the ISB, the centre of the glenohumeral JCS is identical to the centre of the humerus ACS. Movement about the joint has three rotational degrees of freedom. The way that movement is described follows the ISB recommendations (Wu et al., 2005), which differ slightly from traditional anatomical terminology. Together, glenohumeral elevation and plane of elevation specify the amount of arm elevation and in which plane the elevation occurs. As our focus lies on abduction and adduction, all analyses of glenohumeral elevation were conducted in a plane of elevation of 0°, which is roughly equivalent to the coronal plane. Axial rotation specifies internal/external (long axis) rotation and was kept at 0° as well.

Joint excursion measurements were collected after the cadaver was thawed (24 h at temperatures between 5° and 15°) and before dissection began. The scapula was manually stabilized on the thorax by one member of the dissection team while the orientation of the humerus was manipulated. A goniometer was placed at the glenohumeral joint centre to measure passive range of motion (Hammond, 2014; Norkin & White, 2016). The limit of mobility was determined when a certain (admittedly subjective) degree of resistance was met, with care taken to avoid joint damage. Measurements were repeated three times and the mean was taken. The glenohumeral joint in the model was configured to resemble both the joint range of motion recorded during the dissection and the human model (Seth et al., 2019).

2.5 | Muscle-tendon units

MTUs represent either a whole muscle or functionally distinct portions of a muscle, which can be useful when muscles have broad attachment sites. The MTUs characterized in our model and the corresponding MTUs of the human model are listed in Table 1. Decisions about how to model muscles were based on anatomical and experimental observations that suggest different functional roles for different fibre groups (Diogo et al., 2011; Gilroy et al., 2012; Larson & Stern, 1986; Larson et al., 1991; Netter, 2010). To maintain consistency, the abbreviations for the deltoid subunits used in the gorilla model are used to refer to the corresponding subunits of the human model as well.

The supra- and infraspinatus muscles are divided into two subunits in the human model, with one subunit having an origin positioned more superiorly and the other more inferiorly within the supra- and infraspinatus fossae, respectively. We represent these muscles as single units in the gorilla model, with the origin positioned in the centre of their

TABLE 1 Functional divisions of muscle gross anatomy are reported with corresponding muscle-tendon unit (MTU) abbreviations used in the gorilla shoulder model. Abbreviations for human model MTU's follow the names given by Seth et al. (2019)

Muscle (gross anatomy)	MTUs of Gorilla model	MT subunits of gorilla model	Number MTUs	MTUs of Human model	MT subunits of Human model	Number MTUs
Deltoid	Delt		3	Deltoideus		3
Clavicular part		clav	1		Clavicle_A	1
Acromial part		acro	1		Scapula_M	1
Spinal part		spin	1		Scapula_P	1
Supraspinatus	Supraspin		1	Supraspinatus		2
Superior		-	-		A	1
Inferior		-	-		P	1
Infraspinatus	Infraspin		1	Infraspinatus		2
Superior		-	-		S	1
Inferior		-	-		I	1

respective attachment site. Because moment arm is determined by the spatial configuration of the muscle attachments and paths relative to the joint centre, the intermediate origin location of the gorilla muscle units would be expected to result in a moment arm intermediate between the two human subunits (with other factors held constant). In the Results section, we depict the human supra- and infraspinatus moment arms as averages of the two subunits for ease of interspecific comparison. The results with separated subunits are reported in the Supporting Information. Differences in muscle division also affect moment curves, particularly because the mass of a complete muscle is separated into smaller units. To address this issue, the human supra- and infraspinatus moment curves are presented as the sum of both subunits of each muscle. In addition, we used sensitivity analysis to investigate the effects of these differences in supraspinatus and infraspinatus attachments (Text S1, Figures S2 and S3).

2.6 | MTU geometry

Observations on MTU attachments and paths were recorded in surface scans conducted during the dissection (for more information see Text S2). First, muscles were identified with reference to Netter (2010); Diogo et al. (2011); and Gilroy et al. (2012). Next, coloured pins were used to label each muscle unit's origin, insertion and midline. Additional pins were used to label palpable osteological landmarks on each rigid body. After pinning, we used a structured-light surface scanner (Artec Space Spider with Artec Studio 12 software, Artec 3D) to collect three different digital representations of the dissection surface: (a) with the glenohumeral joint fully abducted, (b) fully adducted and (c) in an intermediate position (not quantified). In this way, the three scans capture the change in muscle paths throughout shoulder excursion, as well as an impression of kinematic sequences throughout passive manipulation (Figure S5). The surface scanning process was repeated as the dissection proceeded through progressively deeper muscle layers. Surface scans collected during the dissection were registered to the CT scan and model using the osteological landmarks (Figure S4). A centroid was calculated for each attachment surface and this (x, y, z) point

served as the MTU's origin or insertion. As a result, the specimen-specific muscle attachment sites and pathways observed during dissection could be transferred directly into the model building space (details on the procedure are given in the Supporting Information).

If unconstrained, muscle units running directly from origin to insertion may bisect bones or take paths that are unrealistic for other reasons, because bones are only visualization objects rather than obstacles in the software environment. In OpenSim, this issue is addressed with the insertion of path points (fixed, via or moving) and wrapping surfaces, which constrain the paths muscles take in the null position and throughout joint excursion. We employed two approaches to constraining muscle paths. First, we inserted the same wrapping surfaces and path points present in the existing human model (Seth et al., 2019) into our gorilla model, and then reshaped these features to reflect the morphology of the gorilla skeleton. Next, we examined the resulting muscle paths and compared them to the surface scans for the three different arm elevation positions. To achieve the latter comparison, the dissection surface scans were registered to the model building space. The modelled joint was then moved to imitate the cadaveric glenohumeral positions (Figure S5). This procedure ensured that muscle paths specified in our model corresponded to dissection observations, across joint excursion, for the same specimen. A list of wrapping surfaces used is given in Table 2.

To minimize the influence of allometric scaling, all moment arm lengths (m) and moment values (Nm) are normalized by humerus length (m). The humerus length used in the models was determined as 0.359 m for the gorilla and 0.326 m for the human. Non-normalized moment arms are reported in the Supporting Information. Ideally, moment values would additionally be normalized by body mass. Unfortunately, body mass was not available for the human specimen (Klein Breteler et al., 1999).

2.7 | MTU properties

The four parameters determining the MTU properties are optimal fibre length (l_0^m), pennation angle (θ), muscle physiological

TABLE 2 Muscle wrapping surfaces used in the model, with dimensions

Muscle(s)	Rigid body location	Shape	Dimensions (m)		
			A	B	C
Delt (all)	Scapula	Ellipsoid	0.0465*	0.1007*	0.0496*
Infraspin	Scapula	Ellipsoid*	0.0465	0.1007	0.0496
Infraspin	Humerus	Ellipsoid	0.0306*	0.029*	0.0277*
			Radius	Length	-
Supraspin*	Scapula	Cylinder	0.015	0.0555	-
Supraspin	Humerus	Sphere	0.0289*	-	-

Muscles that use the wrapping surfaces to restrict their paths are given in the first column, (all) refers to all MTUs of a specified muscle.

The asterisk (*) indicates differences to the wrapping surface configuration used in Seth et al. (2019). In their model, the supraspinatus pathway is not constrained by a further wrapping surface attached to the scapula and the infraspinatus wrapping surface on the scapula is a cylinder. Some dimensions were further adjusted to mirror the gorilla specific anatomy.

cross-sectional area (A_{phys}) and tendon slack length (l_g^t). The first three came from dissection, as follows. Tendon slack length (l_g^t) was estimated following the equations of Manal and Buchanan (2004) and using the approach reported in Heers et al. (2018). The estimations are based on MTU length ranges of motion of all degrees of freedom of each joint a muscle spans. OpenSim's Muscle Analysis plotting tool was used to estimate the muscle-tendon length ranges for each MTU of our musculoskeletal model. Muscle pennation angle (θ) influences muscle cross-sectional area and muscle force calculation only for highly pennated muscles ($>20^\circ$, Carlson, 2006; Thorpe et al. 1999; Zajac, 1992). During dissection, deltoid, supraspinatus and infraspinatus muscles were found to not be highly pennate. Therefore, a value of 0° was used as input into the musculoskeletal model. Pennation angle is accounted for in the muscle geometric calculations intrinsic to OpenSim's implementation of a Hill-type muscle model and is therefore not included in A_{phys} calculations (Bishop et al., 2020; Zajac, 1989). After photographs (with visible scale) were taken to measure muscle-tendon length ($\pm 0.1\text{mm}$), the tendon was removed and muscle belly mass of each muscle was measured using an electronic balance ($\pm 0.01\text{g}$). Subsequently, the muscle bellies were digested in 20% nitric acid solution for 24–48 h, a process that also visibly reduced the muscle length (shrinkage). Intact muscle fibres were gently separated and transferred into glycerine-coated petri dishes to terminate the digestion process. The lengths of 10–20 muscle fascicles were measured for each muscle unit on digital photographs, using the measure function in Fiji software (Schindelin et al., 2012). The average of these measured muscle fascicle lengths was corrected for a shrinkage of 43% (Alway et al., 1989; Heron & Richmond, 1993) that was introduced by the nitric acid digestion. This approach resulted in fascicle lengths comparable to those reported in similar studies using different approaches (Table S2). The corrected muscle fascicle length value (L) was assumed to be equivalent to optimal fibre length (l_0^m ; Zajac, 1989). Averaged muscle masses (m_{musc}) and fascicle lengths (L) were calculated for each MTU. We used a muscle density (d) value of $1.06 \times 10^3\text{kg/m}^3$, which has been used as a generalized value for mammalian muscle (Brown et al., 2003; Mendez, 1960; Ward & Lieber, 2005). Muscle cross-sectional area (A_{phys}) was calculated using the following equation:

$$A_{phys} = m_{musc} (Ld)^{-1}$$

We further calculated muscle maximum isometric force capacity F_{max} as:

$$F_{max} = 3.0 \times 10^5 m^{-2} A_{phys}$$

The constant in this equation is specific muscle tension. Similar values were used in other studies on musculoskeletal models in vertebrates, including hominoids (Goh et al., 2017; Hutchinson et al., 2015; O'Neill et al., 2013; Umberger et al., 2003). However, different equations were used to calculate the MTU properties in the human shoulder model that we use for comparison (Nikooyan et al., 2011). To maintain consistency between models, the equations given above were used to recalculate values for the human model, based on the muscle parameters reported by Klein Breteler et al. (1999) and the MTUs described in Seth et al. (2019) (Table S1).

3 | RESULTS

3.1 | Musculoskeletal model parameters

The measured and calculated MTU properties are reported in Table 3. The model together with the rigid body coordinate systems is shown in its zero (reference) position in Figure 4a with all joint angles set to zero. Figure 4b shows the model with the arm in a "resting" position (glenohumeral elevation of 15°) with all muscles visible. Positions between zero and resting position (0° – 15° glenohumeral elevation) are anatomically not feasible, as observed during the range of motion measurements. Therefore, all following analyses start from the resting position. The arm elevation sequence analysed using the musculoskeletal model is shown in the Supplementary Information (Video S1).

3.2 | Moment arm comparison

The deltoid muscle is the main arm abductor in hominoids, traditionally divided into three different functional units. The normalized

TABLE 3 Muscle-tendon units (MTUs) used in the musculoskeletal model (names abbreviated) with properties used for the final analyses

MTU	Muscle mass, m_{musc} (kg)	Fascicle length, L (m)	Pennation angle; θ (°)	Physiological cross-sectional area, A_{phys} (m ²)	Maximum isometric force, F_{max} (N)	Tendon slack length; l_s^t (m)
Delt_clav	0.0633	0.1757	0	0.0003	101.92	0.0113
Delt_acro	0.1662	0.0886	0	0.0018	531.12	0.0703
Delt_spin	0.0567	0.1361	0	0.0004	118.00	0.0443
Supraspin	0.0840	0.0662	0	0.0012	358.66	0.0380
Infraspin	0.1048	0.0839	0	0.0012	353.75	0.0294

moment arms for these three units over arm elevation from the present study and the human model of Seth et al. (2019) are shown in Figure 5 (for absolute values refer to Figure S1). The acromial portion of the deltoid (Delt_acro) shows the greatest similarity in moment arm between species. We found a slightly shorter moment arm in the gorilla model, but with a similarly-shaped curve over glenohumeral elevation.

The moment arm values of the clavicular deltoid (Delt_clav) are smaller in the gorilla model, and the peak shifted towards higher elevation angles. The gorilla model further predicts that the clavicular fibres of the deltoid change function over arm elevation, with the traditional abductor function achieved for glenohumeral elevation beyond about 60°. In less elevated positions, the model predicts a moment arm that would adduct the arm. In contrast, the human model predicts a retention of abduction function for the clavicular fibres throughout glenohumeral excursion, with the peak occurring between about 95–115° of elevation.

Deltoid fibres attaching to the scapular spine (Delt_spin) maintain moment arm values near zero in the human model. In contrast, the gorilla moment arm values are substantial, non-linear and predict a pure adductor function for the spinal deltoid.

The supraspinatus and infraspinatus muscles are components of the rotator cuff. Both muscles enhance arm abduction, external rotation and glenohumeral joint stability. The gorilla infraspinatus moment arm curve is nearly identical to a calculated average of the two human subunit curves (Figure 6) and falls between the curves when the two subunits are plotted separately (Figure S3). Furthermore, sensitivity analyses demonstrate that when the single gorilla infraspinatus origin is moved more superiorly or more inferiorly (to mirror the origins defined for each subunit in the human model), the gorilla curve shifts toward the corresponding human curve (Figure S3). Both models predict an abductor role for this muscle, except at very low elevation angles.

In contrast, the models show a marked difference in supraspinatus moment arm (Figure 6). Abductor moment arm is considerably larger in the gorilla model and the greater magnitude is maintained over a wider range of glenohumeral elevation, only becoming smaller for elevation angles above 95°. In the human model, moment arms are largest at low angles of glenohumeral elevation and reduce consistently. The intermediate moment arm of both subunits loses its ability to act as abductor by 105° of glenohumeral elevation, whereas abductor potential in gorilla is lost only after 135°. Sensitivity analysis shows that the gorilla supraspinatus moment arm remains greater

than the human moment arm, despite shifts in origin location (Figure S2).

The comparison of the total glenohumeral moment arm between the gorilla and human model is shown in Figure 7. While the trend of abductor moment arm changes (the sum of all positive moment arms) is similar in both models, values of the gorilla are generally smaller. Gorilla adductor moment arms (the sum of all negative moment arms) however are generally greater compared to the human model, where values mostly remain close to zero.

3.3 | Comparison of moment-generating capacity

The acromial deltoid possesses the greatest potential for producing abduction moment in both species (Figure 8). This is primarily due to the architectural properties of these MTUs. In both species, the acromial fibres have much higher maximum isometric force values than the clavicular or spinal portions of the deltoid (see Table 3 and Table S1).

The gorilla and human acromial deltoid moment curves differ in the height and location of their peaks. The results suggest that the human Delt_acro is capable of overall higher abduction moment production, and that maximum moment is achieved early in the elevation sequence. However, the human curve falls off precipitously after about 75° of elevation and is no longer capable of moment production beyond about 115°. The gorilla Delt_acro peak is slightly lower overall, and occurs at a higher joint angle. This MTU retains the ability to generate abduction moment across higher elevation angles, until about 135°.

Interspecific differences in moment curves for the other deltoid units are more subtle and follow a similar trend as the moment arm curves. The clavicular deltoid has a lower moment production potential in the gorilla model and its action potential changes across glenohumeral elevation. Moment production potential of spinal deltoid is low for both species (Figure 8). While moment remains close to zero in the human, moment production potential is slightly higher in the gorilla, where spinal deltoid serves as a pure adductor.

Figure 9 shows moment results for the supra- and infraspinatus. The results suggest that the gorilla supraspinatus is capable of generating much greater abduction moments than the human supraspinatus. In the early phases of glenohumeral elevation, the gorilla moments are roughly twice as high as the human values. The human abduction moment production potential decreases thereafter, while the gorilla

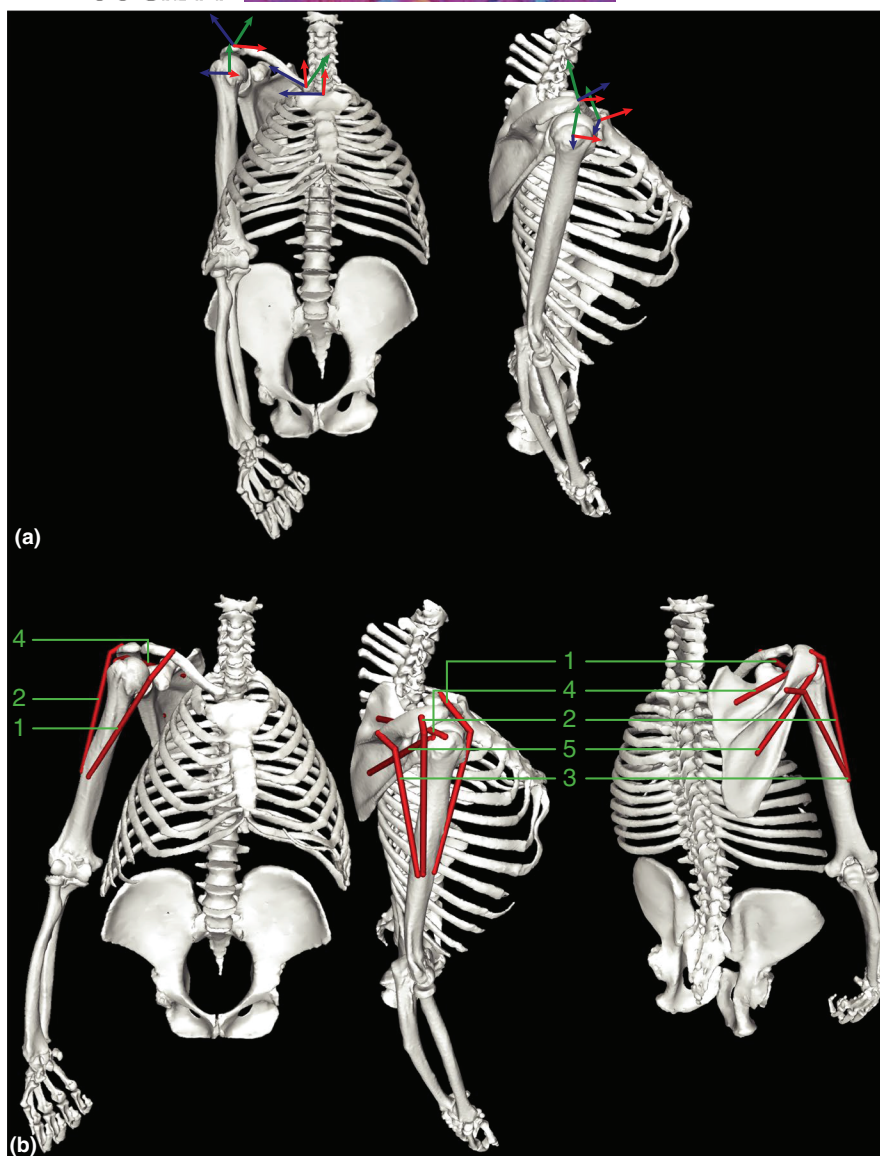


FIGURE 4 Musculoskeletal model of the gorilla. (a) Zero (reference) position of the model, view from frontal (left) and lateral (right). The three axes of the rigid body coordinate systems (ACSs) of the humerus, scapula, clavicle and thorax are displayed, with X-axis in red, Y-axis in green and Z-axis in blue. The origin of these coordinate systems coincide with the origin of the corresponding JCSs. Clavicle ACS not visible in lateral view, for clarity. (b) Muscle-bone configuration of the model, in resting position (arm elevation of 15°). View from frontal (left), lateral (middle) and back (right). Muscles are represented as red bands. 1. Clavicular Deltoid, 2. Acromial Deltoid, 3. Spinal Deltoid, 4. Supraspinatus, 5. Infraspinatus

potential remains high as glenohumeral elevation increases. Between about 70° and 110° elevation, the gorilla supraspinatus moment is up to four times larger than the human values. The marked difference between species stems from the higher maximum isometric force values for the gorilla supraspinatus (see Table 3 and Table S1), amplified by the larger abductor moment arm (Figure 6). Similar to the gorilla supraspinatus moment arm values, moment values remain close to the maximum until a glenohumeral elevation angle of 100° .

With regard to the infraspinatus, the human model suggests higher abduction moment production potential than for *Gorilla*. Within each species, moment production potential of supraspinatus is greater than that of infraspinatus for low elevation angles and vice versa for high elevation angles. However, this transition occurs at

40° of arm elevation in the human model but at 120° in the gorilla model. Furthermore, the species show inverse patterns for supra- and infraspinatus abduction moment production. While supraspinatus is a stronger abductor than infraspinatus in *Gorilla*, the contrary is observed in the human model.

The comparison of the total abductor potential (the sum of all positive moments) for deltoid, supra- and infraspinatus demonstrates similar maxima between the two models (Figure 10). The primary difference between species lies in the degree of glenohumeral elevation where abduction moments are highest. The abductor potential in the gorilla is less than in the human model for low amounts of arm elevation. Beyond elevation angles of 80° , however, moment production potential is distinctively higher in the gorilla.

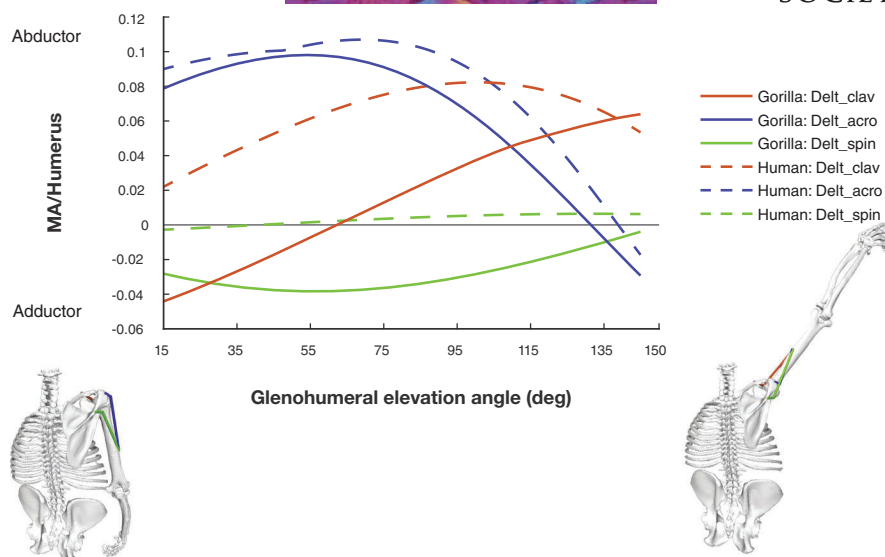


FIGURE 5 Normalized moment arms of deltoid muscle plotted against glenohumeral elevation. Moment arms are normalized by humerus length. The grey solid line separates MTUs acting as abductors (positive moment arms) from those acting as adductors (negative moment arms). See text for details

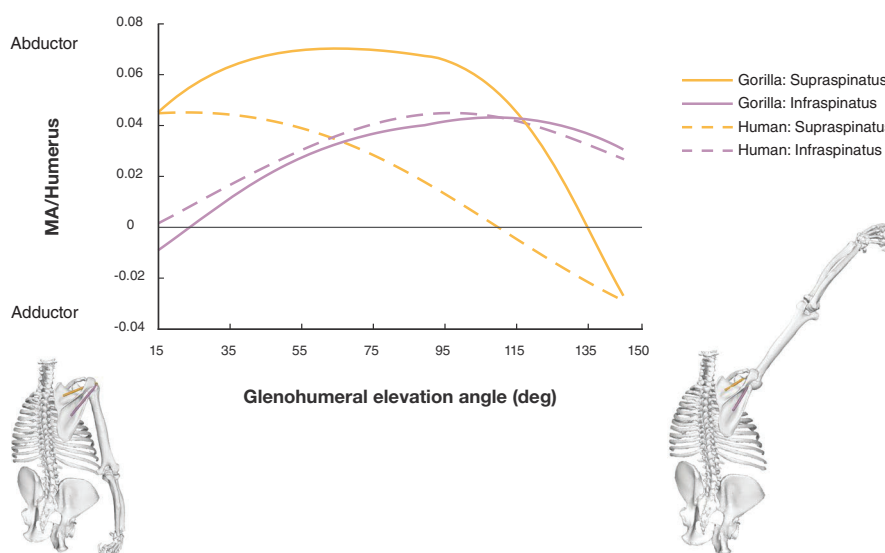


FIGURE 6 Normalized moment arms of supraspinatus and infraspinatus muscle plotted against glenohumeral elevation. Moment arms are normalized by humerus length. The human model moment arm results each represent the mean of the two subunits. The grey solid line separates MTUs acting as abductors (positive moment arms) from those acting as adductors (negative moment arms). See text for details

After elevation angles of 135° , abduction moment potential is small in both models. Total adductor potential (sum of all negative moments) is low for both models throughout their range of elevation motion, but with a slightly higher potential observed in the gorilla.

4 | DISCUSSION

Skeletal differences between gorillas and humans have been linked to a stronger arm-raising mechanism in the former species. This study constitutes the first direct test of this idea. Here, we

presented the development of a three-dimensional musculoskeletal model of a gorilla glenohumeral joint, which was built using data on musculoskeletal geometry and MTU properties collected during a dissection. We combined dissection observations with CT and surface scanning to reflect specimen-specific musculoskeletal properties. The model allows the prediction of MTU moment arm, force and moment production potential for major shoulder muscles crossing the glenohumeral joint. Results from this subject-specific gorilla model were compared to a human shoulder model, to enhance our understanding of arm-raising abilities in non-human apes.

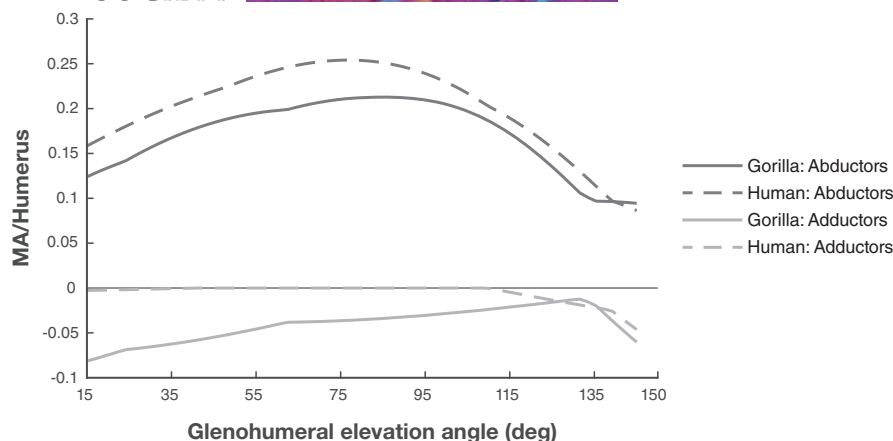


FIGURE 7 Total abductor and adductor moment arms (MA) normalized by humerus length plotted against glenohumeral elevation. Abductor moment arm is the sum of all positive moment arm values calculated for deltoid, supraspinatus and infraspinatus muscles. Adductor moment arm was calculated using negative moment arm values

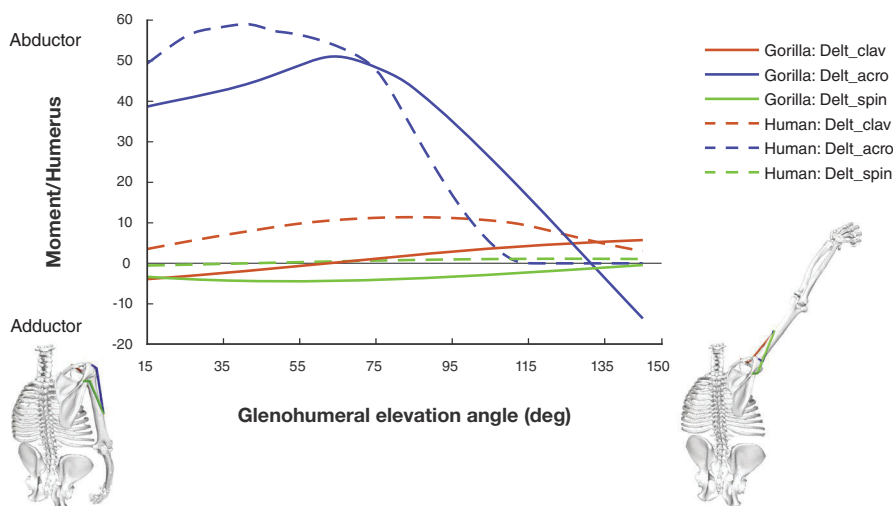


FIGURE 8 Deltoid moment normalized by humerus length plotted against glenohumeral elevation. The grey solid line separates MTUs acting as abductors (positive moment) from those acting as adductors (negative moment). The gorilla model at the bottom visualizes the arm position at 15° and 145° of glenohumeral elevation, respectively

4.1 | Biomechanical performance of glenohumeral abductors

One objective of our study was to investigate whether the biomechanical capacity of glenohumeral abductors is improved in gorillas, compared to humans. Contrary to expectations, our results suggest that gorillas and humans are capable of producing similarly strong glenohumeral abduction, after differences in humerus length are taken into account (see Figure 10). The primary difference between species relates instead to the joint angles where high moments can be generated. While the arm-raising performance is similarly strong in gorilla and human, the gorilla is able to maintain higher abductor moments above 90° of arm elevation, compared to the human without scapular rotation.

We further expected to find support for ideas that link differences in scapular morphology to functional enhancement of arm-raising in gorillas. These hypotheses are cited often in

discussions of hominoid shoulder functional morphology (Green, 2013; Larson, 1993; Potau et al., 2009; Selby & Lovejoy, 2017; Shea, 1986; Sonnabend & Young, 2009; Taylor, 1997) and interpretations of functional capabilities in extinct hominins (Harmon, 2013; Larson, 2013; Melillo, 2016; Ward, 2002), but have never been tested. Interspecific differences in bone shape and skeletal configuration are expected to have the most direct effect on moment arm (Smith & Savage, 1956). Therefore, a functional enhancement due to morphological changes would be evident by greater moment arms and linked to greater moment capacities. However, our results suggest that differences in moment production capacity exist between models, despite minimal differences in moment arms. While total abductor moment potential is greater in gorilla for higher elevation angles, overall abductor moment arms are slightly smaller than in the human model (Figure 7). This implies that soft tissue properties (especially F_{max}) have a great impact on overall glenohumeral abductor capacity. Therefore, our

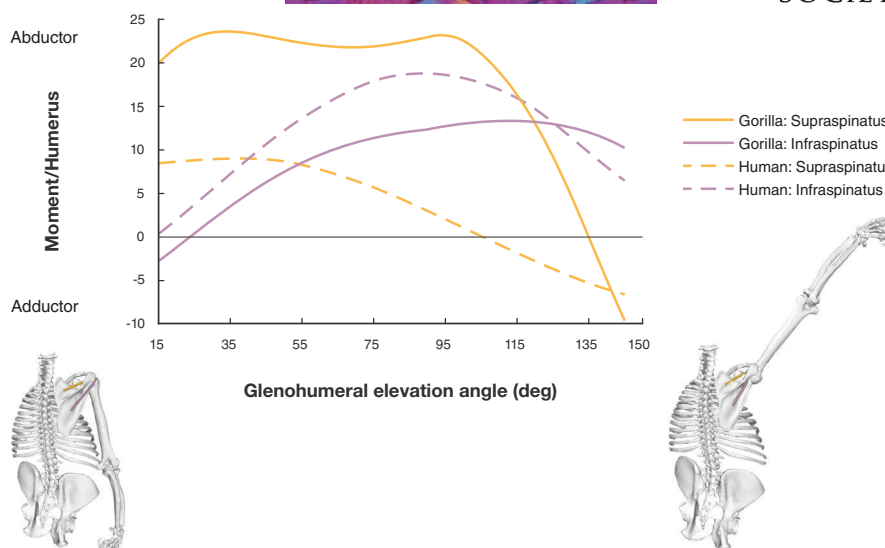


FIGURE 9 Supraspinatus and infraspinatus muscle moment normalized by humerus length plotted against glenohumeral elevation. The human model moment results each represent the sum of the two subunits' moments. The grey solid line separates muscle units acting as abductors (positive moment) from those acting as adductors (negative moment). The gorilla model at the bottom visualizes the arm position at 15° and 145° of glenohumeral elevation, respectively

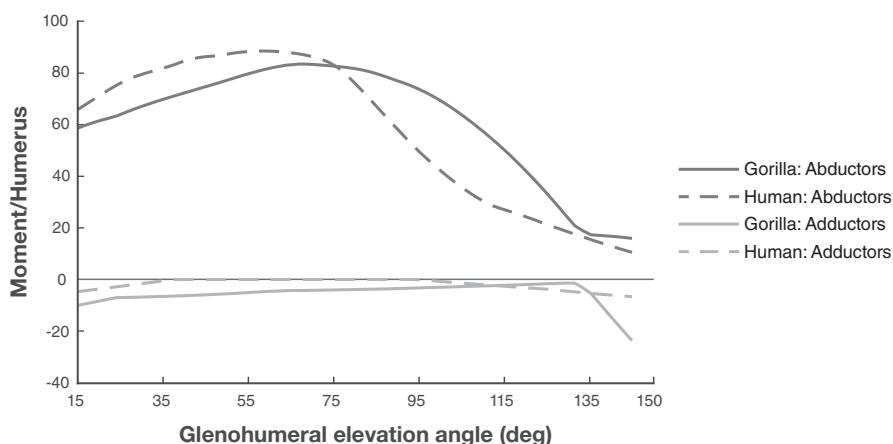


FIGURE 10 Total abductor and adductor moment potential normalized by humerus length plotted against glenohumeral elevation. Abductor moment potential is the sum of all positive moment values calculated for deltoid, supraspinatus and infraspinatus muscles. Adductor moment potential was calculated from all negative values

results highlight the importance of including soft tissue properties in biomechanical analyses. Unfortunately, such data collection is often impossible, especially when studying fossils. Thus, caution has to be applied in cases where the interpretation of biomechanical capabilities is only based on moment arm results, especially in estimating peak moments (e.g. see discussion in Hutchinson et al. 2005 and Brassey et al. 2017).

4.2 | Biomechanical performance of deltoid

Non-human ape morphology was previously understood to enhance function of the deltoid muscle (the main arm abductor) in particular. Specifically, the cranial orientation of scapular spine and greater lateral acromion projection were hypothesized to provide enhanced

deltoid leverage (Corruccini & Ciochon, 1976; Larson, 1993; Miller, 1932; Roberts, 1974).

However, the spinal deltoid, which originates from the scapular spine and inserts onto the deltoid tuberosity in both species, deviates from the expected abductor action in *Gorilla* (Figure 5). Instead, the negative moment arm values suggest a pure adductor action (a morphological tendency to adduct the arm). This difference in moment arm compared to the human model results from a different line of action. In gorillas, the MTU's path runs further caudal to the glenohumeral joint centre due to the oblique orientation of the scapular spine and glenoid (Figure 11). Thus, interspecific differences in scapular spine orientation do not appear to enhance the deltoid abductor ability, but instead change the action of the spinal deltoid from a potential abductor to an adductor role, contradicting earlier hypotheses (Miller, 1932).

Our findings are supported by previous observations on muscle activation during various kinds of movement in apes. Larson and Stern (1986) presented electromyography (EMG) measurements of deltoid activation in chimpanzees during vertical climbing and arm-swinging. The authors found that the activity of the spinal deltoid was out of phase with the other two deltoid units. The clavicular and acromial deltoid were active during phases of arm protraction and abduction during voluntary reaching, vertical climbing, and arm swinging. In contrast, the spinal deltoid was highly active during the support phase and beginning of swing phase, when the arm is already overhead and muscle contraction serves a propulsive function (described by Larson & Stern, 1986 as "propulsive retraction" and adduction). We investigated glenohumeral excursion in the coronal plane, which is only one component of arm movement during arboreal locomotion (Isler, 2005). Future work investigating whether similar differences in moment arm occur during arm elevation in the sagittal plane (pro- and retraction) is necessary. Yet, it is encouraging that our modelling results are consistent with EMG studies suggesting a similar divergence in action between the spinal deltoid and the two other deltoid MTUs.

A more laterally projecting acromion was traditionally understood to enhance leverage of the acromial deltoid. Acromial projection has been linked to enhanced arm raising in hominoids compared to monkeys (Corruccini & Ciochon, 1976; Roberts, 1974) and Ciochon and Corruccini (1977) showed that acromial projection is greater in African apes than in humans. However, our results suggest that despite anatomical differences in acromion shape being present between gorillas and humans, moment arms of acromial deltoid are similar in both species (Figure 5). The model comparison indicates that greater acromial projection in *Gorilla* does not increase the distance between glenohumeral joint rotation centre and this MTU's line of action.

The measurement of acromial projection used by Roberts (1974) and Corruccini and Ciochon (1976), which is called the

coraco-acromial index, quantifies the projection of the acromion lateral to the glenoid, or lateral to a line connecting the tips of the acromion and coracoid (respectively). However, these measurements may fail to capture the structural relationships most relevant to acromial deltoid leverage.

Studies discussing the impact of shoulder morphology on deltoid leverage in humans have long focused on different sets of structural relationships (Howell et al., 1986; Iannotti et al., 1992). These studies have shown that the deltoid moment arm is affected by the amount that the muscle wraps around the humeral head. This wrapping amount is increased where the radius of the humeral head is greater, which is determined laterally by the greater tubercle projection. Therefore, it is not the acromion projection relative to glenoid (Ciochon & Corruccini, 1977; Corruccini & Ciochon, 1976; Craik et al., 2014), but rather the relationship between acromion projection and greater tubercle projection that is more relevant to deltoid leverage (Rietveld et al., 1988). The latter is described by Nyffeler et al. (2006) as the acromion index. This biomechanically important parameter has not been quantitatively addressed in comparative studies across hominoids. Additionally, the radius of the non-spherical humeral head differs across its circumference due to the protruding greater and lesser tubercles. In the musculoskeletal models, this was addressed by using an ellipsoid wrapping surface for the deltoid (Table 2). As the deltoid spans most of the humeral head in a broad sheet, we expect some variation of wrapping and moment arm across the muscle depending on the path around the ellipsoid. This could be addressed in future analyses by dividing the deltoid MTU into smaller subunits. Future analyses would further benefit from incorporating measurements of scapular and corresponding humeral morphology.

Despite the similar moment arms, acromial deltoid moment production potential is different between the gorilla and human model (Figure 8). Therefore, these differences are related to the soft tissue properties. When scapula rotation is prohibited, humans are unable

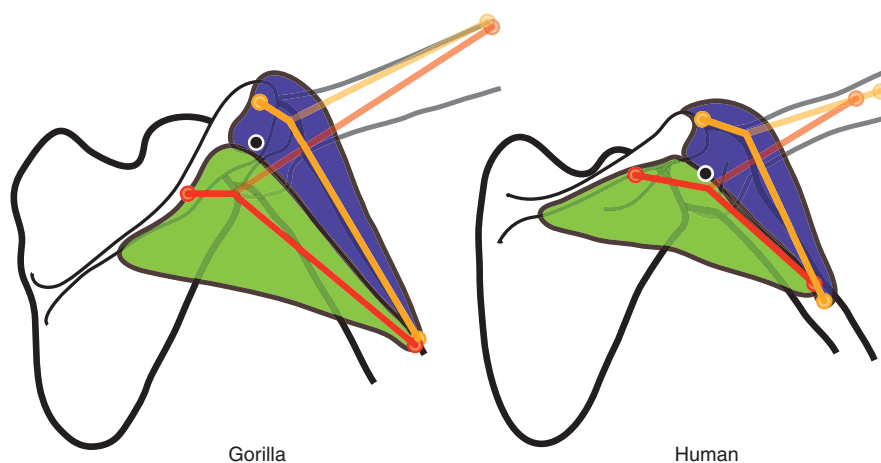


FIGURE 11 Acromial and spinal deltoid MTU path in gorilla (left side) and human (right side). The distance between glenohumeral rotation centre (black-white circle) and spinal deltoid MTU path (red line) is greater in the gorilla than in the human model, but similar for acromial deltoid (orange line). Acromial (blue) and spinal deltoid (green) muscles are visible for glenohumeral elevation angles of 35°. MTU paths and humerus shape are displayed for glenohumeral elevation angles of 35° (darker) and 105° (lighter)

to lift their arm above 90° (Inman et al., 1944). Lucas (1973) suggested the reason for this to be the force-length relationship of the acromial deltoid. Without scapular rotation, Lucas (1973) proposed that the fibres of the human deltoid would not be able to shorten any further and therefore not produce force, beginning at approximately 90° of glenohumeral elevation. He further suggested that the scapular rotation mechanism prevents this problem. As the scapula rotates cranially, the acromion process of the scapula (deltoid origin) shifts medially, away from the humeral insertion. Thus, a certain distance between origin and insertion points is maintained as glenohumeral abduction occurs, keeping the deltoid muscle fibres closer to their optimal muscle fibre length and allowing the deltoid to maintain its moment production potential. Because differences in scapular rotation may exist between humans and gorillas (see Introduction), but the magnitude and nature of these differences remain unclear, our models compared joint function without scapular rotation. In line with expectations, the human model predicted a loss of moment production capacity at about 100° abduction (Figure 8). Our results suggest that such a scapular rotation mechanism may be of less importance in the gorilla, as the acromial deltoid muscle fibres are able to continue producing force with the arm further overhead. These findings add further support to the idea of Tuttle and Basmajian (1977) that scapular rotation is of less importance in non-human apes due their cranial orientation of the glenoid cavity, a configuration that is only achieved after full scapular rotation in humans.

The moment arm of the clavicular deltoid also predicts a difference in action between species (Figure 5). While moment arm results suggest a pure abductor action in human clavicular deltoid, results from the gorilla model indicate a change in action from adductor to abductor with arm elevation. Similar to the spinal deltoid, this change in action stems from a difference in muscle path (relative to location of the glenohumeral joint centre) between species. In the human model, the line of action of clavicular deltoid generally runs superior to the glenohumeral joint rotation centre, due to a lateral orientation of glenoid. In *Gorilla* however, the line of action is positioned inferior to joint centre early in glenohumeral elevation. This difference in position of the muscle path relative to the joint centre follows from the cranial orientation of glenoid and clavicle, and causes the observed negative (adductor) moment arm. With increasing elevation angles, the muscle path shifts further cranially and thereby sits superior to the joint centre after 60° of elevation, which causes the change in anatomical tendency (action). In this way, differences between gorillas and humans in clavicle and glenoid orientation affect the biomechanics of clavicular deltoid, but not in a manner that improves gorilla abductor potential.

Larson and Stern (1986) observed a similar potential to change action in the clavicular deltoid. During their studies on muscle activation, they found that the clavicular deltoid was active during swing and, to a lesser extent, during support phases of vertical climbing. Therefore, the study concluded that the clavicular portion of the deltoid is both able to elevate and retract the arm, depending on arm position. These EMG observations are consistent with our prediction that clavicular deltoid has the potential to switch between

adductor and abductor action in apes, depending on glenohumeral joint angle.

4.3 | Biomechanical performance of supraspinatus and infraspinatus

Our analysis suggests that supraspinatus is able to produce much greater normalized abduction moment in *Gorilla* than *Homo* (Figure 9). This is consistent with Miller (1932), who argued for greater supraspinatus abduction moment in non-human apes and suggested that the enhancement would arise from the obliquely oriented scapular spine. Miller suggests a twofold enhancement: (a) an obliquely oriented scapular spine leads to a widening of the supraspinous fossa, providing a larger attachment surface to a more massive muscle capable of generating greater force, and (b) “increases the abduction power of that muscle by providing it with a more advantageous mechanical location above the head of the humerus.” The comparison of dissection data reported here and by Klein Breteler et al. (1999) yields a greater supraspinatus muscle size in *Gorilla* than *Homo*, which allows for a higher maximum isometric force capacity (Table 3 and Table S1). Other researchers have also reported comparatively large masses for the *Gorilla* supraspinatus (Bello-Hellegouarch et al., 2013; Larson, 2015; Larson & Stern, 2013). In accordance with Miller (1932), our findings supported the idea that a more massive supraspinatus muscle, associated with a larger supraspinous fossa, contributed to comparatively greater abduction moment in *Gorilla*.

Supraspinatus moment arm is also relatively larger in the gorilla than in the human model (Figure 6), demonstrating that supraspinatus abduction moment is additionally enhanced biomechanically. Our findings support Miller's assumption of a mechanical advantageous configuration. Contrary to Miller (1932), however, differences in scapular spine orientation do not appear to drive the difference in moment arm. An oblique orientation of the scapular spine in *Gorilla* is associated with a more inferior position of the supraspinatus origin, and thus a more oblique line of action. The inferior shift in origin location reduces the distance between this muscle's line of action and the joint rotation centre, thereby reducing moment arm considerably early in arm elevation and providing only slight enhancement in later arm elevation (Figure S2). Furthermore, our sensitivity analysis indicates that a more oblique line of action, as resulting from a cranially oriented scapular spine, does not improve supraspinatus moment arm over arm elevation. Our findings suggest that musculoskeletal changes associated with an oblique scapular spine lead to a reduction in supraspinatus moment arm, rather than an increase. Lee et al. (2020) made a similar observation by estimating supraspinatus moment arm during arm abduction for a large sample of morphologically variable humans. They also found an association between a more oblique spine orientation and reduced moment arm. Therefore, we suggest that a more cranially oriented scapular spine does not biomechanically enhance supraspinatus abduction moment in gorillas.

Earlier studies showed that moment arm is more sensitive to small changes in attachment sites closest to the joint rotation centre (Bates et al., 2012; Goh et al., 2017; Murray et al., 2002; O'Neill et al., 2013). In case of the supraspinatus muscle, insertion sites on the greater tubercle of the humerus are closer to joint centre than origin sites on the supraspinous fossa of the scapula. A superimposition of the shoulder bones and supraspinatus muscle attachment sites on glenohumeral joint centre (Figure 12) highlights that the distance between insertion site and joint rotation centre is greater in the gorilla than in the human model. This greater distance corresponds to a higher degree of lateral projection of greater tubercle in the gorilla. Therefore, it appears that the difference in supraspinatus moment arm between models is primarily influenced by differences in humerus morphology, specifically the radius of the humeral head and the degree of lateral projection of the greater tubercle.

The infraspinatus insertion site on the greater tubercle is increased and shifted more cranially in *Pan* and *Gorilla* compared to all other hominoids (Arias-Martorell, 2018). The infraspinatus muscle path further differs in *Gorilla* compared to *Homo*, due to differences in scapular spine and glenoid orientation. Despite these evident differences in anatomy however, the infraspinatus moment arm is highly similar between the human and gorilla model (Figure 6). Therefore, our results indicate that skeletal modifications of scapula and humerus, and changes in muscle path do not lead to greater infraspinatus abductor leverage in *Gorilla*, compared to *Homo*.

The infraspinatus fossa is relatively smaller in gorillas than humans. While this evidently has no effect on the moment arm, it reflects a reduction in infraspinatus muscle mass and PCSA (Bello-Hellegouarch et al., 2013; Larson, 2015). This reduction leads to a

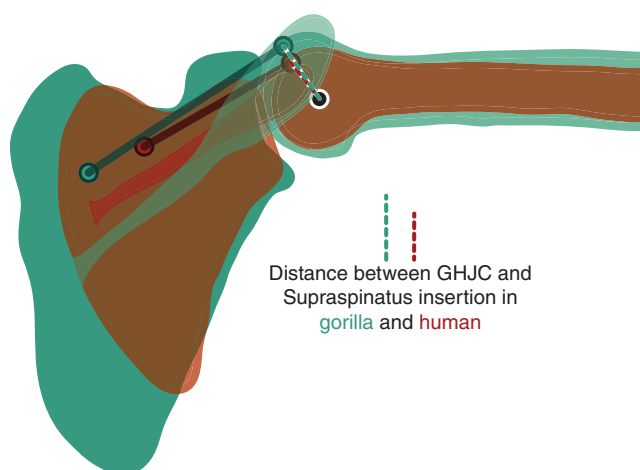


FIGURE 12 Impact of greater tubercle projection on distance between supraspinatus insertion and glenohumeral joint centre (GHJC). Shape of scapula and humerus of gorilla (in blue) and human (in brown) were superimposed to GHJC (black-white circle). The superimposition highlights the greater distance (dashed lines) between GHJC and supraspinatus insertion site (coloured circles) in gorilla. Attachment site on the scapula has a lesser effect on the line of action. Position of the humerus relates to 95° of glenohumeral abduction

reduced maximum isometric force capacity in *Gorilla* (see F_{\max} values in Table 3 and Table S1). As a result, abductor moment potential is less in the gorilla, than in the human model (Figure 9), despite similar moment arm values. Thus, gorilla shoulder morphology does not enhance infraspinatus abduction potential, but is instead increased in humans due to soft tissue properties.

4.4 | Study Limitations

The musculoskeletal model presented here was designed to closely reflect the anatomical features recorded during the dissection. Therefore, this specimen-specific model does not capture intraspecific variability present in *Gorilla*. The study individual died of old age, so some amount of muscle wasting likely occurred. However, this would not be expected to affect moment arm results markedly. Furthermore, the data informing the human model were also collected from an older individual (Klein Breteler et al., 1999), rendering the soft tissue properties more comparable. As body mass measurements were not available for the human model, moment could not be normalized by body mass or weight. Human men between 50 and 59 years were found to have masses between 63.5 and 126.7 kg with a mean of 90.5 kg (Fryar et al., 2016). The female western lowland gorilla of this study falls below this mean, with a mass of 80.5 kg. Therefore, the moment results normalized by humerus length might actually underestimate the results for the gorilla model. While great care was taken to collect the data and build the model in a way most similar as described for the human model (Klein Breteler et al., 1999; Nikooyan et al., 2011; Seth et al., 2019), different assumptions made during the model-building process cannot be excluded.

The comparison of our measurements and model results is difficult due to a lack of studies analysing and reporting similar parameters. Until now, only Kikuchi and Kuraoka (2014) and Payne (2001) reported soft tissue properties of a gorilla shoulder. However, their data were collected from male gorillas. As size differences are great between sexes (Remis, 1998), more data from female gorillas are needed for comparison (but see Supporting Information and Table S2 for a more detailed comparison of MTU properties). Furthermore, no empirical measurements of muscle moment arms over arm ab-/adduction (e.g. tendon travel experiments; An et al., 1984) exist for gorilla shoulder muscles. Within non-human great apes, only Thorpe et al. (1999) reported moment arms of shoulder muscles. The authors measured deltoid moment arm statically on a male subadult chimpanzee. Their measurement of 3.3 cm falls within range of our acromial deltoid moment arm estimates. However, dynamic moment arm studies that include simultaneous measurements of arm position are needed for gorillas. We nonetheless expect validation of our model outputs from such studies, given the care taken to collecting our data and the successes with prior studies integrating experimental and theoretical calculations (Ackland et al., 2008; Brown et al., 2003; Hutchinson et al., 2015; Murray et al., 1995).

This study concentrated entirely on arm abduction potential of glenohumeral muscles. Accordingly, the analysis focused on arm elevation in the coronal plane, with long-axis rotation kept at 0°. However, this limitation of glenohumeral joint is artificial and does not aim to reflect arm-raising kinematics of humans or gorillas during natural movement sequences. Kinematic studies of various arboreal locomotion have shown that shoulder kinematics are highly three-dimensional and thereby emphasized the great shoulder flexibility in hominoids (Isler, 2002, 2005; Thompson et al., 2018). Since moment arm is dependent on joint position, we can expect moment arm results to differ when glenohumeral elevation in other planes and long-axis rotation are included into the analysis. This study further concentrates on rotation about the glenohumeral joint, which constitutes only one of the four shoulder joints that take part in human arm elevation. Additionally, the analysis was restricted to simulate moment arm and moment results of the main glenohumeral abductors. To provide greater insight into the relationship between shoulder biomechanics and morphology, future research would benefit from taking further shoulder muscles and motion around all four shoulder joints into consideration. A benefit of computer models such as ours is that such motions can be combined or separated to untangle their individual influences on biomechanical outputs.

We further want to emphasize that our results do not suggest that gorillas and humans are similarly strong. Here, we mainly tested for a mechanical advantage due to differences in shoulder configuration and additionally included soft tissue parameters to estimate muscle moment capacities. However, more variables influence muscle performance like maximum shortening velocities, fibre type composition and muscle activation (O'Neill et al., 2017; Scholz et al., 2006), which have not been considered in our analysis.

The focus of hominoid shoulder studies has long been on linking a particular pattern of shoulder morphology to advantages in glenohumeral abduction. However, our investigation did not demonstrate a clear link between these features specific for non-human ape scapulae and stronger glenohumeral abduction capacity. While most ideas had previously focused on the deltoid, biomechanical advantages were found in the supraspinatus, but these abduction moment differences appear to be more closely related to proximal humerus morphology than to scapular morphology. Contrary to previous ideas, the very marked morphological differences between human and non-human ape scapulae, which clearly co-vary with function, appear to be related to arm-lowering more than arm-raising. Future research may benefit from focusing on how bone morphology, particularly scapula shape, affects other functions of glenohumeral rotation (especially adduction and protract/retraction outside the scapular plane) and scapular rotation—movements that are also central to arboreal locomotion and knuckle walking.

5 | CONCLUSION

In this study, the link between shoulder morphology and biomechanical enhancement of arm-raising in humans and gorillas was

examined. We found the glenohumeral abduction potential of deltoid, supraspinatus and infraspinatus is of similar magnitude between gorillas and humans. The results cast significant doubt upon long-standing proposals that link scapular features characteristic of arboreal primates, such as a cranially oriented scapular spine and glenoid, to biomechanical enhancement of glenohumeral abductors (Ashton & Oxnard, 1964; Corruccini & Ciochon, 1976; Miller, 1932; Roberts, 1974). Instead, our findings suggest that gorilla-specific shoulder morphology does not enhance glenohumeral abduction moment capacity. However, our analyses demonstrate that abduction potential across arm elevation is greater in *Homo* at low amounts of arm elevation, but greater in *Gorilla* with the arm elevated above the head. These differences are mainly achieved by variation in muscle force-production and force-length properties. While no skeletal enhancement of deltoid abduction potential was observed in *Gorilla*, supraspinatus abduction moment capacity was found to be greater, enhanced by greater muscle force and leverage compared to *Homo*. However, improved leverage does not result from a more cranial scapular spine orientation as suggested by Miller (1932). Instead, we propose that increased lateral projection of the greater tubercle in gorilla provides a biomechanical enhancement of supraspinatus abduction moment capacity. As this study constitutes the first test of biomechanical enhancement due to shoulder morphology in hominoids, further analyses including additional shoulder muscles and joints are necessary.

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AUTHOR CONTRIBUTIONS

Julia van Beesel carried out the dissection, built the model, analysed the data and drafted the manuscript. Stephanie Melillo designed the project, organized and assisted in the dissection as well as data analysis and co-wrote the manuscript. John Hutchinson helped with the model-building process, with data analysis and with improving the manuscript. Jean-Jacques Hublin provided funding and guidance for the direction of this study as well as comments on the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are partially available in the article and Supporting Information and are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Chapter 2

Comparison of the arm-lowering performance between *Gorilla* and *Homo* through musculoskeletal modeling

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ORIGINAL ARTICLE

Comparison of the arm-lowering performance between *Gorilla* and *Homo* through musculoskeletal modeling

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Abstract

Objectives: Contrary to earlier hypotheses, a previous biomechanical analysis indicated that long-documented morphological differences between the shoulders of humans and apes do not enhance the arm-raising mechanism. Here, we investigate a different interpretation: the oblique shoulder morphology that is shared by all hominoids but humans enhances the arm-lowering mechanism.

Materials and methods: Musculoskeletal models allow us to predict performance capability to quantify the impact of muscle soft-tissue properties and musculoskeletal morphology. In this study, we extend the previously published gorilla shoulder model by adding glenohumeral arm-lowering muscles, then comparing the arm-lowering performance to that of an existing human model. We further use the models to disentangle which morphological aspects of the shoulder affect arm-lowering capacity and result in interspecific functional differences.

Results: Our results highlight that arm-lowering capacity is greater in *Gorilla* than in *Homo*. The enhancement results from greater maximum isometric force capacities and moment arms of two important arm-lowering muscles, teres major, and pectoralis major. More distal muscle insertions along the humerus together with a more oblique shoulder configuration cause these greater moment arms.

Discussion: The co-occurrence of improved arm-lowering capacity and high-muscle activity at elevation angles used during vertical climbing highlight the importance of a strong arm-lowering mechanism for arboreal locomotor behavior in nonhuman apes. Therefore, our findings reveal certain skeletal shoulder features that are advantageous in an arboreal context. These results advance our understanding of adaptation in living apes and can improve functional interpretations of the hominin fossil record.

KEYWORDS

gorilla locomotion, hominoid shoulder, moment arm, musculoskeletal model, shoulder functional morphology

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1 | INTRODUCTION

Variation in primate shoulder anatomy is well-documented. Comparisons of shoulder morphology across the order Primates have identified major structural differences that distinguish most hominoids and suspensory monkeys from the other species (Miller, 1932; Inman et al., 1944; Ashton & Oxnard, 1964; Roberts, 1974; Corruccini & Ciochon, 1976; Ciochon & Corruccini, 1977; Larson, 1993; Larson, 1995; Young, 2008; Schmidt & Krause, 2011). For instance, the scapula of suspensory primates is characterized by elongated vertebral and axillary borders, a more obliquely oriented spine and glenoid, and an acromion that projects well beyond the glenoid. These structures provide attachment sites for the scapular rotators and humeral abductors, which are the muscle groups primarily responsible for arm-raising in humans (Ashton & Oxnard, 1963; Ashton & Oxnard, 1964; Inman et al., 1944; Lucas, 1973). Therefore, earlier studies focused on linking these specific scapular morphologies to hominoid reliance on using the arms overhead in an arboreal setting, especially during vertical climbing and forelimb suspension (Keith, 1923; Schultz, 1936a; Schultz, 1936b; Oxnard, 1967; Jenkins et al., 1978; Larson, 1993). In this way, the shared-derived scapula features listed above were understood to be advantageous in arboreal settings as they were thought to enhance the arm-raising mechanism in particular. This form-function relationship established through comparisons of the primate scapulae were then used to infer overhead reaching and climbing adaptations in a variety of mammals that exhibit similar scapular morphology (Astúa, 2009; Oxnard, 1968; Sears, 2005), including extinct hominin species (Green & Alemseged, 2012; Haile-Selassie et al., 2010; Larson, 2013; Melillo, 2016). However, recent evidence has cast doubt on these ideas.

The focus on the arm-raising mechanism alone as an explanation for scapular shape is controversial. Studies conducted in the 1960's highlighted that apes are distinguished not only by strong arm-raising muscles, but also by larger and stronger muscles that flex the elbow and lower the arm (Ashton & Oxnard, 1963; Ashton & Oxnard, 1964; Napier, 1963; Oxnard, 1963; Oxnard, 1967). Later, studies extensively characterized the musculoskeletal system of the gibbon shoulder (Michilsens et al., 2009; Michilsens et al., 2010). They found that, while most shoulder muscles have high force-generating capacities, masses of the abductor muscles were much lower, which resulted in the lowest force production capacity among the arm muscles studied (Michilsens et al., 2009). Additionally, biomechanical analyses of siamangs demonstrated that shoulder adductors have significantly greater muscle moment arms (MAs) than abductors. Their results indicated that, within the species, adductors, rather than abductors, are built for moment-generation (Michilsens et al., 2010).

We recently compared the arm-raising performance of the glenohumeral abductors in *Gorilla* and *Homo* and failed to find support for the arm-raising hypothesis (van Beesel et al., 2021). Instead, we found that an oblique scapula shape and obliquely oriented clavicle in *Gorilla*, traditionally understood to enhance arm-raising, negates the ability of the clavicular and spinal deltoid to act as abductors. Due to

this oblique morphology, the path and line of action of these deltoid muscle-tendon units (MTUs) run more caudally relative to a more cranially positioned glenohumeral joint (GHJ) center. As a result, these muscles would adduct the arm in *Gorilla*, in contrast to the abduction action capability in humans. Previously published electromyographic (EMG) studies had already provided experimental evidence for the presence of those functional differences between apes and humans. Larson and Stern (1986) showed that the posterior deltoid is active during arm-lowering phases while climbing. This observation led them to propose that this muscle was contributing to body propulsion by raising the body's center of mass—consistent with our musculoskeletal model results. Our findings provided an explanation for that observed functional difference, by indicating how differences in scapular shape and clavicle orientation changed action capability. Therefore, we proposed that *Gorilla*-specific shoulder morphology, compared to *Homo*, enhances the arm-lowering mechanism, rather than the arm-raising mechanism. However, we previously identified this insight in an investigation of muscles traditionally thought of as glenohumeral abductors (van Beesel et al., 2021). In this study, we focus on muscles traditionally classified as arm adductors and retractors.

'Arm-lowering', which we use to describe any decrease in elevation angles at the GHJ, is an important mechanism in the propulsive phases of various locomotor modes in gorillas and other nonhuman hominoids. During suspensory locomotion, arm adduction and retraction propels the swinging body up- and forward, which produces greater acceleration (Larson & Stern, 1986; Stern et al., 1980). In quadrupedal walking, arm retraction is used to pull the body over the supporting limb (Pontzer et al., 2014; Simpson et al., 2018). In vertical climbing, arm retractors are highly active (as evidenced by EMG data) during the support phase (Fleagle et al., 1981; Larson & Stern, 1986; Stern et al., 1980), when the body is elevated through a combination of arm retraction, abduction and elbow flexion (Isler, 2005). Studies of comparative anatomy found that muscles active in this phase are enlarged in nonhuman apes compared to monkeys (Ashton & Oxnard, 1963; Ashton & Oxnard, 1964; Napier, 1963; Oxnard, 1963; Oxnard, 1967). The importance of arm-lowering for ape locomotion gives further reason to expect that an enhanced arm-lowering mechanism would be beneficial.

Here, we test for the idea that the arm-lowering performance is enhanced in *Gorilla* compared to *Homo* by investigating relevant biomechanical metrics such as moments and MAs. This study focuses on *Gorilla*, an ape genus that exhibits all of the shared-derived shoulder morphological features discussed above. This investigation will further our understanding of *Gorilla* adaptation and the shared adaptations of apes more generally.

A moment is a metric of how well a muscle might be able to transform force into limb rotation (Michilsens et al., 2010). Therefore, it is a measure of musculoskeletal performance for a given task. Moments are the product of muscle-tendon force and muscle MA. The MA can be measured as the perpendicular distance between the MTU line of action and axis of rotation. Some musculoskeletal software such as OpenSim use an alternative "virtual work" approach similar to the tendon-travel method that allows for more advanced 3D computation

(Channon et al., 2010; Delp et al., 2007; Delp & Loan, 2000; Hutchinson et al., 2015), based on the amount of MTU length change per unit of rotation (Sherman et al., 2013). MA is a measure of how effectively linear muscle force is converted to moment and is dependent on the musculoskeletal geometry (MTU attachments and path). The sign of a MA indicates if a muscle would act to increase or decrease the joint angle. Therefore, MA also quantifies the action a MTU can produce (Pandy, 1999).

Musculoskeletal models are virtual reconstructions of a musculoskeletal system that can be used to estimate muscle moments and MAs for different types of movement (Seth et al., 2018). Here, we add the humeral adductor and retractor muscles *teres major*, *teres minor*, *subscapularis* and *pectoralis major* (clavicular and sternal parts) to the previously described gorilla musculoskeletal model (van Beesel et al., 2021). We then calculate muscle MA and moment-generating capacity for arm-lowering in different planes of elevation, to cover a greater range of arm movement that could be exploited during different locomotor types. We compare our results to those of an already existing human shoulder model (Seth et al., 2019). Our analysis focuses on rotations about the GHJ. Therefore, performance differences in arm-lowering are evaluated regarding the ability to reduce glenohumeral elevation angles. However, three additional shoulder joints are known to contribute to arm movement in humans: the acromioclavicular joint, the sternoclavicular joint and the scapulothoracic joint. In our species, the mechanism of arm-raising and lowering is well studied, and scapulothoracic joint movement is known to contribute up to one third to the total arm-raising movement (Codman, 1934; Duprey et al., 2015; Lucas, 1973). In nonhuman apes, the role of scapular motion during arm movement is the subject of ongoing investigation. While a recent study showed that the acromion is cranially displaced during vertical climbing in chimpanzees (Thompson et al., 2018), the specifics of scapula rotation in apes remains largely conjectural. Due to the high degree of uncertainty regarding scapular range of motion in nonhuman hominoids, we focus our biomechanical analysis on GHJ rotation while keeping the scapula stable. This decision mainly affects our analysis of *pectoralis major*, as MA and therefore moment about the GHJ would be expected to differ with a change in scapular position and orientation. Therefore, the reference or zero position of the gorilla model was selected with great care, to facilitate comparability with the human model while maintaining species-specific differences in scapular position (van Beesel et al., 2021).

We predict that *Gorilla* arm-lowering muscles will exhibit larger, negative MAs and greater moment-generating capacity than *Homo*. Greater negative MAs would provide evidence for a morphology-induced enhancement of arm-lowering. Greater moment capacities would indicate that *Gorilla*-specific musculoskeletal shoulder configuration – soft and hard tissue properties combined – contribute to a general enhancement of the arm-lowering mechanism, compared to *Homo*. Such enhancement could indicate that arm-lowering is a significant mechanism in the locomotor habits of gorillas, like quadrupedal walking and climbing, that are not habitually exploited by humans. We review the MAs and moment capacity estimations over arm-lowering

using previously published kinematic and EMG data of nonhuman apes during quadrupedal walking and vertical climbing. We expect that arm-lowering enhancement in *Gorilla* compared to *Homo* occurs at elevation angles used during typical nonhuman ape like locomotor types and where the respective muscles are known to be active. Such findings would be consistent with the idea that gorilla shoulder morphology (and by extension, nonhuman ape shoulder morphology more generally) reflects locomotor adaptations via the arm-lowering mechanism.

2 | MATERIALS AND METHODS

We investigated MAs and moment-generating capacities of muscles crossing the GHJ using two musculoskeletal shoulder models that were built for use in the open-source software OpenSim (Delp et al., 2007; Seth et al., 2018). The human model was developed by Seth et al. (2019) and the initial development of the gorilla model was described in van Beesel et al. (2021). Here, we extended the gorilla model by adding further MTUs crossing the GHJ (Table 1). Data informing the model were collected in the course of CT scanning and dissecting a gorilla cadaver. These data include various kinds of information on joint geometry, MTU geometry and muscle architectural properties (Figure 1). We summarize this procedure below and additional details can be found in van Beesel et al. (2021) and in the Supporting Information (section 1).

2.1 | Subject and dissection notes

Observations informing our model were collected through dissecting a female western lowland gorilla (*Gorilla gorilla*) in April 2019. The cadaver was acquired ethically through a collaboration with the Cleveland Museum of Natural History, Erie Zoo and Cleveland Metroparks Zoo. The specimen was euthanized at the age of 48.8 years after suffering from age-related illnesses. A body mass of 80.5 kg was determined during necropsy. The fresh-frozen cadaver was CT scanned and dissected afterwards.

The CT scanning took place at the Ohio State University College of Veterinary Medicine. The scan (voltage: 120 kV; current: 319 mA) was acquired using a Revolution Evo Lightspeed CT (GE Healthcare, Waukesha, WI, USA) and reconstructed at voxel size $0.977 \times 0.977 \times 0.525$ mm. We used the scan to capture the articulated configuration of the upper body skeleton. Meshes of the ribcage with vertebral column, humerus, scapula, and clavicle were generated in Avizo software (version 9.3.0, Visualization Sciences Group, Burlington, MA, USA), using a threshold approach. Afterwards, the meshes were decimated and smoothed in Geomagic Studio® (version 2013, RSI 3D-Systems). The meshes were imported into Autodesk Maya software (version 2019, Autodesk), where they were reorganized into a hierarchical skeleton and the GHJ (position and orientation of axes) was defined (see below). Following Bishop et al. (2021), the virtual skeleton was used as bone and joint geometry input in the gorilla

TABLE 1 Muscle gross anatomy is represented by muscle-tendon units (MTUs) or functionally divided into smaller muscle-tendon subunits (MTSUs) in the gorilla (van Beesel et al., 2021) and human (Seth et al., 2019) musculoskeletal model. The gorilla MTUs and MTSUs detailed here are new additions to the gorilla musculoskeletal model

Muscle (gross anatomy)	MTUs of gorilla model	MTSUs of gorilla model	Number MTUs	MTUs of human model	MTSUs of human model	Number MTUs
Teres major	TeresMaj		1	TeresMajor	–	1
Teres minor	TeresMin		1	TeresMinor	–	1
Subscapularis	Subscap		1	Subscapularis		3
Upper		–	–		S	1
Middle		–	–		M	1
Lower		–	–		I	1
Pectoralis Major	PecMaj		2	PectoralisMajor		3
Clavicularis		Clav	1		Clavicle_S	1
SternocostalisSuperior		–	–		Thorax_M	1
SternocostalisInferior		Sternocost	1		Thorax_I	1

musculoskeletal model (van Beesel et al., 2021), and to acquire muscle geometry data (Supporting Information section 1). Bones of the lower arm and hand are included for visualization purposes only.

2.2 | Joint geometry

Our analysis of muscle MAs and moments considers arm movement about the GHJ. The development of the model GHJ is described in van Beesel et al. (2021) for the gorilla and in Seth et al. (2019) for the human model. The gorilla GHJ was reconstructed following the same rules and guidelines used for the human model to facilitate comparability. In the following, we highlight the most important characteristics, which apply to the GHJ in both models. The gorilla reference or null position (rotation around all axes is zero) was defined in Autodesk Maya (version 2019, Autodesk) and was arranged similar to the null position in the human model. In the reference position, the coronoid fossa faces ventrally and the humerus long axis is parallel to the sagittal and coronal plane and intersects the thorax as a result (Figure 1a). Thus, the model reference position is not intended to be a biologically plausible posture. We report MA and moment results for biologically plausible joint positions only. The center of the humeral anatomical coordinate system coincides with the center of the humeral head and the orientation of the anatomical axes are defined based on anatomical landmarks of the humerus following the recommendations of Wu et al. (2005) (Figure 1a). Similarly, the definition and order of rotation follows the ISB recommendations (Wu et al., 2005). The three rotational degrees of freedom (DOFs) of the GHJ, in rotational order, are plane of elevation (plane_elv, anatomical y-axis), shoulder elevation (shoulder_elv, anatomical x-axis) and long axis rotation (axial_rot, floating axis), as described by Seth et al. (2019). Therefore, rotations about the plane of elevation and long axis rotation cause a rotation about the humeral longitudinal axis (Figure 1b). The three translational DOFs were held fixed and rotations about the long axis rotation were kept at 0° in the gorilla and human models in all analyses herein. The

range of motion around each rotational axis was limited based on measurements of passive arm manipulation performed during the dissection and is the same in both models. We further focus the presentation of the results on elevation angles greater than zero. While negative elevation angles, like hyperextension, involve plausible joint positions, kinematic observations highlight that these are not used during typical locomotor behaviors (Isler, 2005; Pontzer et al., 2014), and were therefore omitted from our analysis.

The orientation of the plane of elevation determines the plane in which the arm is elevated. A plane of elevation of 0° corresponds to arm elevation in the frontal plane (ab-/adduction), a plane of 90° corresponds to elevation in the sagittal plane (pro-/retraction). The MA and moment values are reported for arm elevation in elevation planes of 0°, 30°, 60°, and 90°. Due to the intersections with the thorax mentioned above, biologically plausible joint positions differ with plane of elevation. MA and moment are reported for elevation angles between 13° and 145° in a plane of 0°, 24° and 145° in a plane of 30°, 44° and 145° in a plane of 60° and 59° and 145° in a plane of 90° (Figure 1b). The arm elevation in the four different planes used in the biomechanical analyses is shown in Video 1.

2.3 | MTU performance (MA and moment analyses)

Model outputs reported in this study include predictions of MA and moment production capacity. Muscle MA predictions are particularly affected by MTU geometry. Estimations of moment production capacity are determined by MTU architectural properties and by MA. MTU architectural properties and geometry data of the arm-lowering muscles, newly added to the gorilla model in this study, were collected during the dissection. MTU attachment points and paths were determined by combining observations and 3D images taken during the dissection with the CT scan data (Figure 1c, d). MTU architectural properties including muscle mass, fiber length and pennation angle

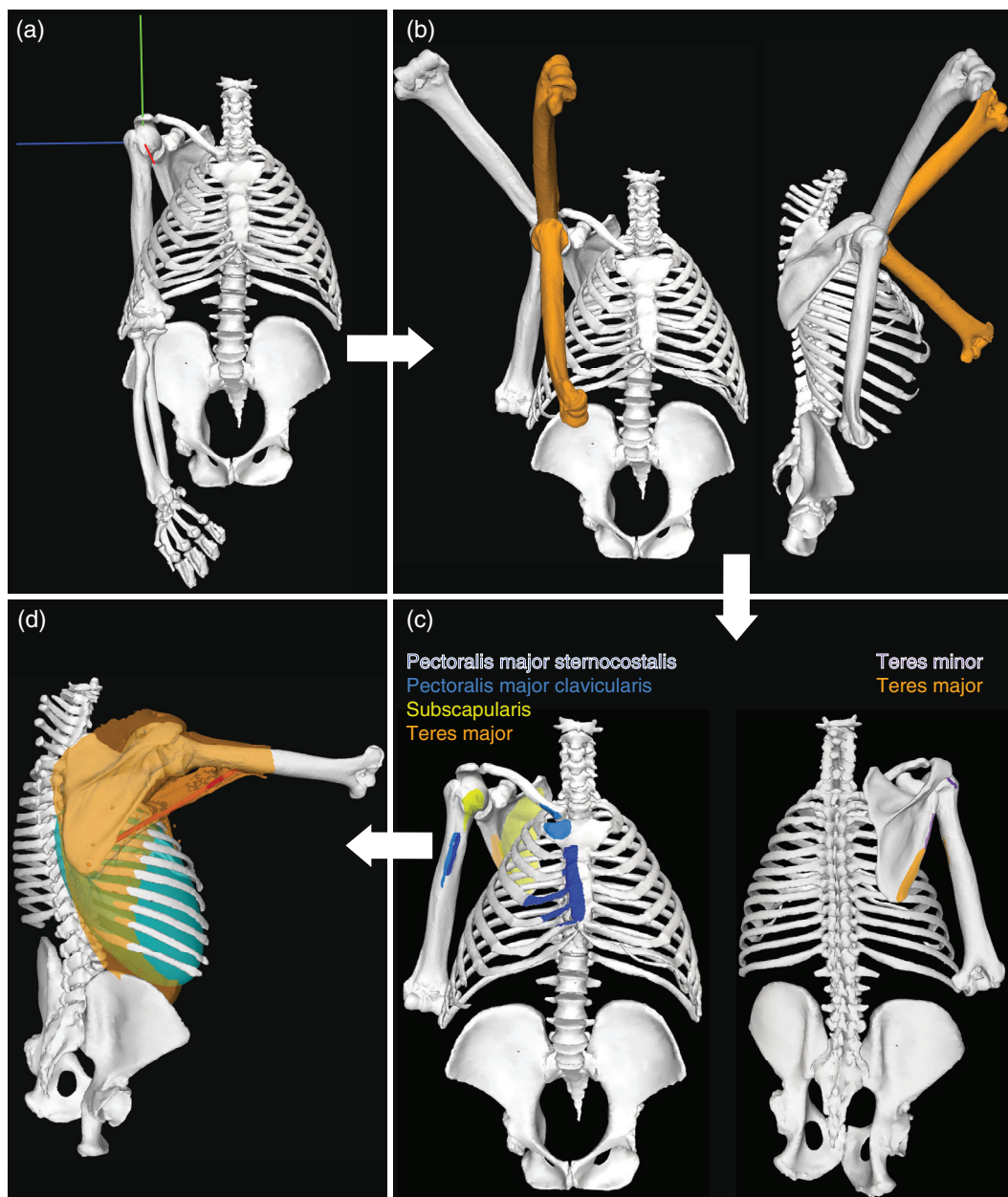


FIGURE 1 Workflow of model editing. (a) View from the front, model is in zero position (all joint angles set to zero). Axes of the humeral anatomical coordinate system are displayed, x-axis in red, y-axis in green, z-axis in blue. (b) Minimum and maximum shoulder elevation in the elevation planes of 0° (white) and 90° (orange) used in the analysis, with axial_rot fixed at 0°. View from the front (left) and side (right). (c) Muscle attachment sites on thorax, clavicle, scapula and humerus. View from the front (left) and from back (right) with attachment sites highlighted. (d) Model with arm position mirroring that of the surface scan (orange), which is used to evaluate muscle wrapping of teres major (red line). The thorax-wrapping surface (blue) is used to prevent teres major from intersecting with the thorax

were measured as each muscle was removed during the dissection. These data were used to calculate maximum isometric force (F_{\max}) and to estimate tendon slack length. We follow the approach originally described in van Beesel et al. (2021), and details are provided here in the Supporting Information (section 1).

We present MA and moment results for each of the muscles listed in Table 1. The values were estimated using the muscle analysis plotting tool of OpenSim. The moment predictions incorporate information on F_{\max} capacity, MAs and force-length assumptions

(Zajac, 1989). Active muscle fiber force was calculated using the Millard et al. (2013) equilibrium muscle model. Therefore, moment capacity estimations considered active and passive forces. The active fiber forces of teres major and pectoralis major are presented in the Supporting Information (section 2). We report the MA results normalized by maximum humerus length, which is 0.359 m for the gorilla and 0.326 m for the human. Moment results are reported normalized by humerus length times body mass^{2/3}, assuming that muscle force is proportional to areas, and hence mass^{2/3} (Jaric et al., 2002). The gorilla

specimen had a dead mass of 80.5 kg. Unfortunately, the body mass of the male human specimen could not be measured directly (Klein Breteler et al., 1999). Thus, body mass was estimated using the estimated total body length of 168 cm (Klein Breteler et al., 1999) and the average body mass index of 26.8 that is reported for a contemporary population of men in a similar age group (Statistisches Bundesamt Deutschland, 2001), producing an estimated body mass of 75.6 kg. The results are presented in graph format as curves tracking MA or moment values in different elevation planes across the specified range of GHJ angles (see Joint Geometry).

During the model building process, a decision has to be made whether a muscle is represented by a single MTU or divided into smaller muscle-tendon subunits (MTSUs). The decision mainly affects muscles with broad attachment sites, as MTUs and MTSUs are modeled using attachment points, not surfaces. For some muscles considered in this study, these decisions were made differently for the human and gorilla models. Table 1 compares the MTU and MTSU divisions in both models, and details the differences in pectoralis major and subscapularis subdivision. For ease of comparison between models, MA results are presented as mean values of all subunits of a MTU and moment results as the sum of the MTSU values. As pectoralis major and subscapularis have broad origin sites, divisions into different numbers of MTSUs mainly affect origin positions. We used a sensitivity analysis to address how modeling decisions about attachment positions and number of divisions affect the MA predictions of both muscles. Detailed information and results of the sensitivity analysis are presented in the Supporting Information (section 3).

2.4 | Musculoskeletal test configurations

Morphological differences between gorillas and humans affect muscle attachment positions, muscle paths, and thus MAs. The modeling approach allowed us to exchange anatomical parameters in order to disentangle which morphological aspects of the shoulder affect arm-lowering MAs and result in interspecific functional differences. We focused our analysis on teres major and pectoralis major, because they are among the most important muscles involved in arm-lowering and body propulsion (Ashton & Oxnard, 1963; Gray & Lewis, 1918). We evaluated the clavicular and sternocostal pectoralis major MTSUs separately, because they originate from different bones and thus might be independently affected by interspecific differences in skeletal configuration. The effects on muscle MA are presented for elevation planes of 0° and 90°, as these encompass the overall observed patterns.

We altered each model in order to investigate the effects of musculoskeletal differences. The gorilla humerus was isometrically scaled to the size of the human humerus, while preserving the relative muscle insertion points. This size-adjusted humerus together with the preserved insertion positions was then added to the human model. The inverse procedure was repeated with the human humerus to replace the humerus in the gorilla model. This transposition allowed us to investigate and disentangle the degree to which humerus morphology

specifically affects the biomechanical performance of the arm-lowering mechanism, compared to the morphology of the combined thorax and shoulder girdle.

3 | RESULTS

3.1 | Model construction and evaluation

The architectural properties of the MTUs added to the gorilla musculoskeletal model (van Beesel et al., 2021) and those of the human model (Seth et al., 2019) are reported in Table 2. Generally, the calculated F_{\max} values that are normalized by body mass^{2/3} are higher in the gorilla than in the human model. The single exception is the teres minor, for which the human model F_{\max} is nearly two times higher than in the gorilla model. The difference in normalized F_{\max} values between models is highest in the subscapularis muscle, which can produce more than twice the amount of force in the gorilla compared to the human. Furthermore, the subscapularis muscle has the greatest force-generating capacity in both models.

A comparison of muscle architectural properties reported here and in other ape studies is presented in the Supporting Information (section 1 and Table S3). Generally, the calculated architectural properties of our gorilla specimen fall within the range observed in other nonhuman apes (Carlson, 2006; Kikuchi et al., 2012; Kikuchi & Kuraoka, 2014; Oishi et al., 2009; Payne, 2001; Thorpe et al., 1999). However, F_{\max} normalized by body mass^{2/3} was small compared to adult chimpanzees and male gorillas. These findings could be related to differences in muscle biology based on sexual dimorphism within *Gorilla* and allometric scaling patterns between gorillas and chimpanzees. Alternatively, the difference may be due to the poor health status of our study subject at the time of death. Additional observations on female gorillas are needed to further investigate these alternatives.

The spatial reconstruction of MTU attachment points and paths are presented in Figure 2. As MA is sensitive to attachment positions, we evaluated the relative insertion positions of teres major and pectoralis major to those reported by other studies. The comparison shows that the spatial reconstruction lies within the range previously observed in African apes. The results confirm that nonhuman apes have more distal humeral insertion positions of teres major and pectoralis major than observed in the human model (see Supplementary Information section 1 and Table S2 for more details).

The range of glenohumeral elevation angles in the four different planes used in the following biomechanical analyses is shown in Video 1.

3.2 | Teres major and minor

Normalized MA and moment results for teres major and minor are reported in Figure 3. MA curves are similar across elevation planes in both muscles and in both species (Figure 3a). These results suggest that the efficacy and function of these muscles is not strongly

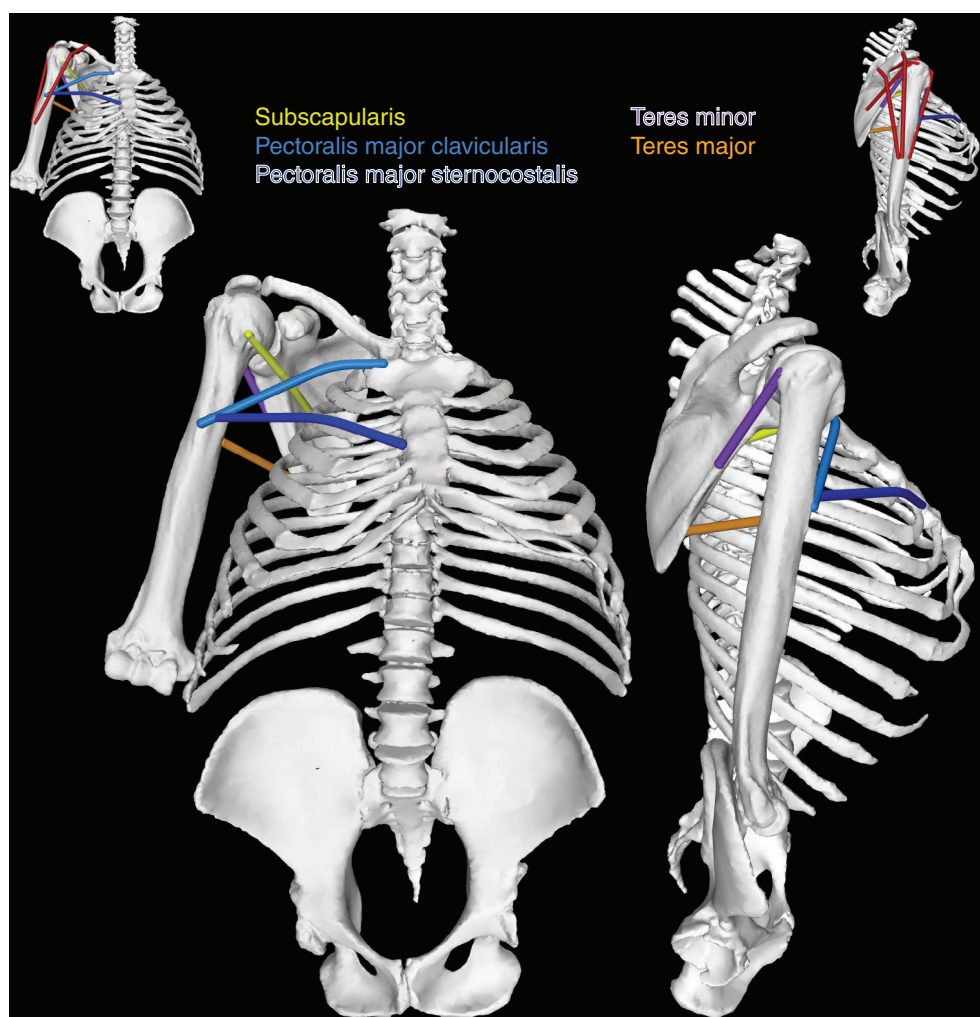
TABLE 2 Muscle architectural properties calculated for the muscle-tendon units (MTUs) and muscle-tendon subunits (MTSUs) of the gorilla and human model. Abbreviations given in Table 1 are used

Gorilla model	m_{musc} (kg)	L(m)	θ (°)	Norm F_{max}	l_s^t (m)	Human model	Norm F_{max}
TeresMaj	0.1028	0.1190	0	2.860	0.0467	TeresMajor	2.394
TeresMin	0.0252	0.0795	0	1.048	0.0089	TeresMinor	1.970
Subscap	0.2391	0.0622	18.4	12.728	0.0652	Subscapularis	5.647
						Subscapularis_S	1.514
						Subscapularis_M	1.736
						Subscapularis_I	2.397
PecMaj				5.475		PectoralisMajor	4.668
PecMajClav	0.0794	0.1198	0	2.196	0.0273	PectoralisMajorClavicle_S	1.145
PecMajSternocost	0.1080	0.1092	0	3.279	0.0741	PectoralisMajor-Thorax_M	1.919
						PectoralisMajor-Thorax_I	1.604

Note: Maximum isometric force (F_{max}) is normalized by body mass^(2/3) to facilitate comparison. For MTUs with subdivisions, the normalized sum of F_{max} values of the MTSUs is given additionally.

Abbreviations: m_{musc} , muscle mass; L, fiber length; θ , pennation angles; l_s^t , tendon slack length.

FIGURE 2 Gorilla musculoskeletal shoulder model with added muscles. View from the front (left) and side (right). Muscles are represented as colored bands. The smaller models (top) display the full set of shoulder muscles of the gorilla model (with muscles previously defined in red). Model shown in resting position (arm elevation of 15°)



affected by the plane in which the arm is raised. In both species, the largest negative MA values are predicted when the arm is in a lowered position and the curves course upward the higher the arm is elevated. However, there is a marked difference in the magnitude of teres major

MAs between models. The larger negative values suggest that gorilla-specific musculoskeletal geometry makes the teres major more effective in arm-lowering in all planes. Across all muscles studied here, the greatest arm-lowering MAs are predicted for the gorilla teres major.

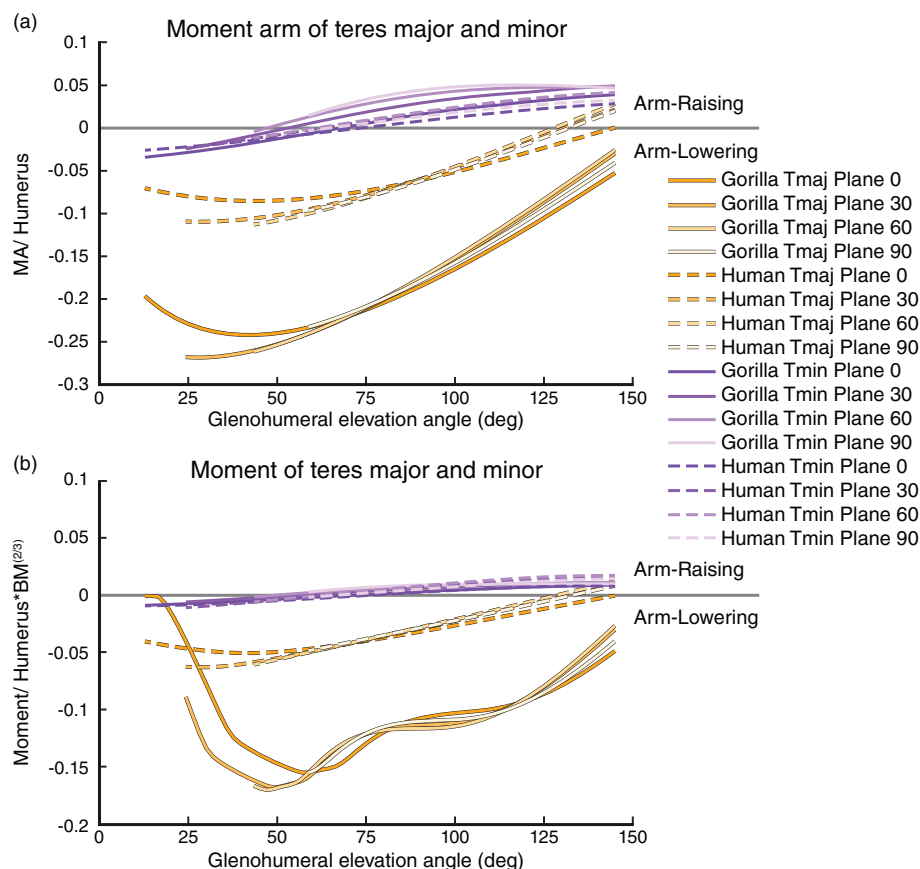


FIGURE 3 MA normalized by humerus length and moment normalized by humerus length times body mass^(2/3) of teres major (Tmaj) and minor (Tmin) muscle. Positive values predict an arm-raising, negative values an arm-lowering action of the MTUs

Additionally, the gorilla teres major MA values remain markedly negative throughout glenohumeral elevation, indicating that muscle activation results in arm-lowering action in all considered positions. In teres minor however, both models predict a shift in action capability from arm-lowering to arm-raising over the course of increasing arm elevation.

Overall, the moment curves are similar to the MA curves for both models (Figure 3b). *Gorilla* teres major moment-generating capacity is enhanced through greater MAs and active fiber forces across elevation angles between 30° and 80° compared to *Homo* (Figure 3 and Figure S2 [a]). As no active force can be developed for smaller elevation angles, moment-generating capacity is reduced. Across higher angles, *Gorilla* teres major moment capacity is higher compared to *Homo*. Overall, *Gorilla* moment capacity is mainly enhanced by greater MAs and further supported through greater F_{max} and force-generating capacities (Table 2).

Teres minor moment-generating capacity is similar in the gorilla and human models. Although MA values are slightly larger in the gorilla model, a smaller gorilla F_{max} value results in a moment curve indistinguishable from the human model. Maximum arm-raising moment capacity is predicted for high arm elevation angles.

3.3 | Pectoralis major

Pectoralis major MA changes with elevation angle and elevation plane in both models (Figure 4a). The results indicate that pectoralis major

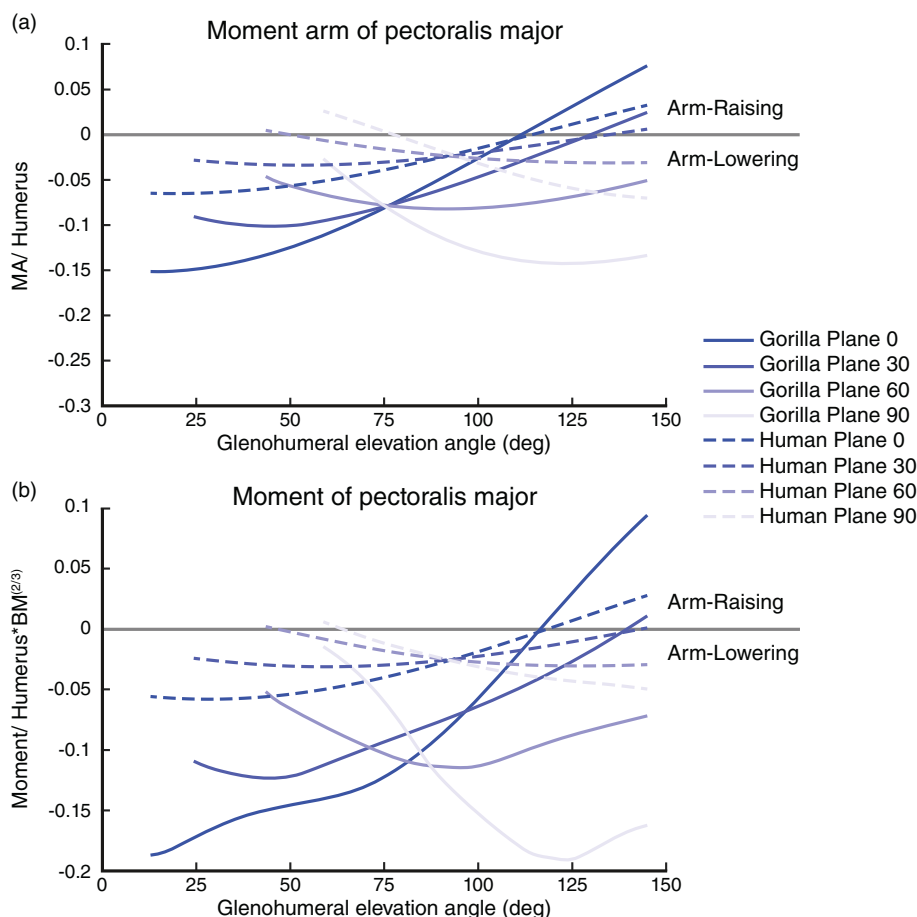
action capability is highly dependent on arm position. In the elevation planes 0° and 30°, the muscle has a large arm-lowering MA when the arm is in a lowered position, whereas in the planes 60° and 90° large arm-lowering MAs occur when the arm is in an elevated position. Additionally, in an elevation plane of 0° the muscle is able to act as an arm-raising muscle in both models (elevation angles above 110°), whereas in an elevation plane of 90° the muscle has an arm-raising action capability only in the human model (plane 90°, elevation angles below 75°). Similar to teres major, there is a marked difference in the magnitude of the mean pectoralis major MAs between the models, with the MAs estimated in the same elevation plane being generally larger (more negative or positive) in the gorilla than in the human model.

Estimated pectoralis major moments are larger in the gorilla than the human model (Figure 4b). The between-model differences in moment are more pronounced than those in MA. These enhanced differences result from a disparity in force-generating capacities (Figure S2 [b]), particularly from a greater F_{max} potential in the gorilla model (Table 2).

3.4 | Subscapularis

MA and moment results suggest similar arm-lowering performance of subscapularis in *Gorilla* and *Homo* (Figure 5). Like in the teres major and minor, differences between elevation planes are small. A general

FIGURE 4 MA normalized by humerus length and moment normalized by humerus length times body mass^(2/3) of pectoralis major muscle. Positive values predict an arm-raising, negative values an arm-lowering action of the MTUs



arm-lowering action is predicted for both models and in all planes. Overall, MA remains relatively constant over the course of arm elevation (Figure 5a).

Although the gorilla subscapularis muscle has the highest F_{max} capacity (Table 2) of all muscles analyzed in this study, moment capacity predictions are small (Figure 5b). The small moment predictions result from the relatively small subscapularis MA.

3.5 | Evaluating the effects of musculoskeletal geometry using test configurations

The results above show that the gorilla model exhibits larger arm-lowering MAs for multiple MTUs. Those larger MAs result from differences in the overall musculoskeletal geometry. In order to investigate the extent to which species-specific differences in MA are due to thorax and shoulder girdle morphology vs. humerus morphology, we compared the original models to test configurations in which components of the models were swapped. In Figures 6 and 7, images 1 and 4 depict the original models. Image 2 depicts a test configuration where the gorilla thorax and shoulder girdle musculoskeletal geometry were combined with the size-adjusted human humerus musculoskeletal geometry. Image 3 depicts the inverse test configuration, where the human thorax and shoulder girdle musculoskeletal geometry were

combined with the size-adjusted gorilla humerus musculoskeletal geometry.

3.5.1 | Teres major and the sternocostal portion of pectoralis major

In both original models, teres major and the sternocostal portion of pectoralis major have a muscle path oriented from inferomedial (origin) to superolateral (insertion) (model illustrations in Figure 6a and b, compare configuration 1 and 4), but the degree of muscle path orientation and thus MA differ between models. Comparing images of the original models and test configurations highlights the fact that the orientation of the muscle path is affected most strongly by humerus morphology and insertion location. In test configuration 2, the gorilla scapula exhibits a cranially oriented glenoid fossa. However, the muscle insertion located proximally on the human humerus shaft generates a muscle path that is overall very human-like in being strongly inferomedially to superolaterally inclined (compare images 2 and 4 in Figure 6 [a and b]). A comparison of test configurations 1 and 3 highlights the inverse: when the laterally directed glenoid and muscle origins of the human model are combined with the gorilla humerus morphology and muscle insertions, an overall gorilla-like muscle path results.

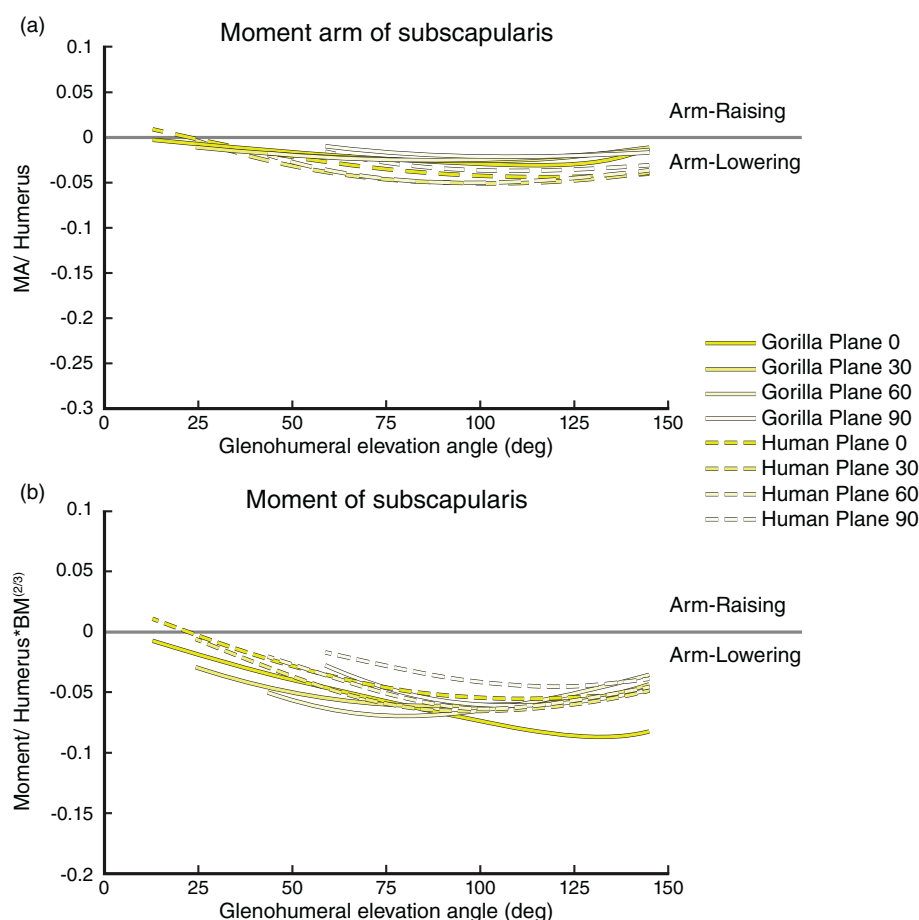


FIGURE 5 MA normalized by humerus length and moment normalized by humerus length times body mass^(2/3) of subscapularis muscle. Positive values predict an arm-raising, negative values an arm-lowering action of the MTUs

The moment arm curves quantify the effect of altering humerus musculoskeletal geometry. The solid pink curves trace the large negative MAs of the original gorilla model. The solid green lines, representing test configuration 2, show that MA is greatly reduced by introducing the human humerus morphology with its proximal muscle insertion to the gorilla model. Comparison of the dashed MA curves illustrates the inverse: MAs of the human model (green dashed lines) are increased with the addition of the gorilla humerus and distally located muscle insertion. The effect is greatest in teres major in both planes and in pectoralis major in a plane of 0° for elevation angles below 100°, as well as in pectoralis major in a plane of 90° (elevation angles above 75°).

The comparison of these test configurations highlights that the humerus morphology and muscle insertion location have the most pronounced effect on MA in teres major and sternocostal pectoralis major.

Thorax and shoulder girdle morphology have a lesser, though still notable effect on teres major MA. This is evident when comparing the test configurations that use similar humerus musculoskeletal geometries but different scapula musculoskeletal geometries (Figure 6 (a)). Those test configurations using the gorilla scapula musculoskeletal geometry result in higher arm-lowering MAs than those using the human scapula musculoskeletal geometry (comparison of solid pink to dashed pink and solid green to dashed green curves). This effect is likely due to scapula morphology. The cranially oriented glenoid

increases the distance between the GHJ center and the teres major muscle line of action and thus enhances the arm-lowering MA in the gorilla.

The effect of thorax and shoulder girdle morphology on sternocostal pectoralis major is somewhat different (Figure 6b). Here, test configuration 3 (pink dashed curves), which combines the human thorax and shoulder girdle musculoskeletal geometry with the gorilla humerus morphology, enhances arm-lowering MA compared to the original gorilla model (pink solid curves). However, in an elevation plane of 90° the difference between the effect of the human and gorilla thorax and shoulder girdle morphology on muscle MA becomes less significant the higher the elevation angles. Overall, the more cranial orientation of the GHJ center relative to muscle origin, which is caused by the cranial oriented glenoid and cranial position of the scapula on the thorax, has a negative effect on the gorilla sternocostal pectoralis major arm-lowering MA. However, this negative effect is small compared to the arm-lowering MA enhancement due to the gorilla humerus musculoskeletal morphology.

3.5.2 | Clavicular portion of pectoralis major

In both original models and contrary to teres major and sternocostal pectoralis major, the muscle path of the clavicular portion of pectoralis major is oriented from superomedial (origin) to inferolateral (insertion)

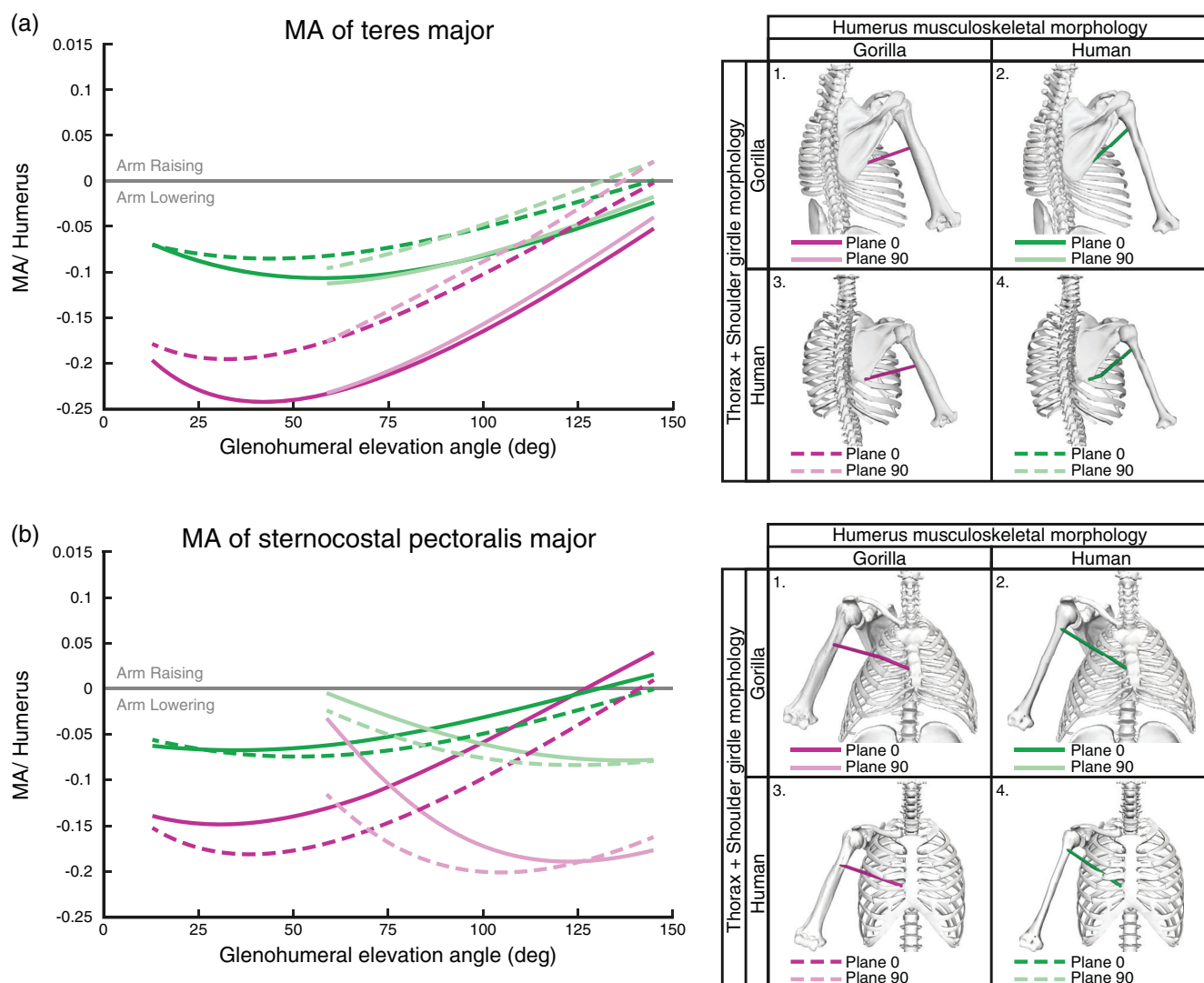


FIGURE 6 Biomechanical consequence of shoulder morphological variation for teres major (a) and sternocostal pectoralis major (b). The line style separates the gorilla (solid) from the human (dashed) thorax and shoulder girdle morphology, while the line color separates the gorilla (pink) from the human (green) humerus morphology. MAs estimated in an elevation plane of 0° are in darker color; in an elevation plane of 90° are in lighter color. The model pictures (right side) highlight the different combinations of musculoskeletal morphologies used in the test configurations. MA estimates are normalized by humerus length

(model illustrations in Figure 7, configuration 1 and 4). However, the degree of muscle path orientation and thus MA differ between models. The comparison of the images of the original models and test configurations highlights that muscle path orientation is most strongly affected by thorax and shoulder girdle musculoskeletal geometry. In test configuration 3, the gorilla humerus exhibits a distally located muscle insertion. However, the lateral glenoid orientation and muscle origin position generate a muscle path that is overall very human-like in being strongly superomedially to inferolaterally inclined (compare images 3 and 4 in Figure 7). A comparison of images 1 and 2 highlights the inverse: when the humerus musculoskeletal geometry and the proximal muscle insertion of the human model are combined with the gorilla thorax and shoulder girdle musculoskeletal geometry, an overall gorilla-like muscle path results.

The moment arm curves quantify the effect of altering thorax and shoulder girdle morphology. The dashed green curves trace the MAs of the original human model. The solid green curves, representing test configuration 2, show that the arm-lowering MA is enhanced by introducing the gorilla thorax and shoulder girdle morphology with a muscle origin concentrated on the sternum and a cranially oriented glenoid. Comparison of the pink MA curves illustrates the inverse: MAs of the gorilla model (pink solid curves) are reduced by introducing the human thorax and shoulder girdle musculoskeletal geometry (test configuration 3, pink dashed curves) with its more lateral clavicular origin and lateral oriented glenoid. However, in the elevation plane of 90° test configuration 3 (light pink dashed curves) predicts greater, more negative arm-lowering MAs at elevation angles above 120° than the original gorilla model (light pink solid curves).

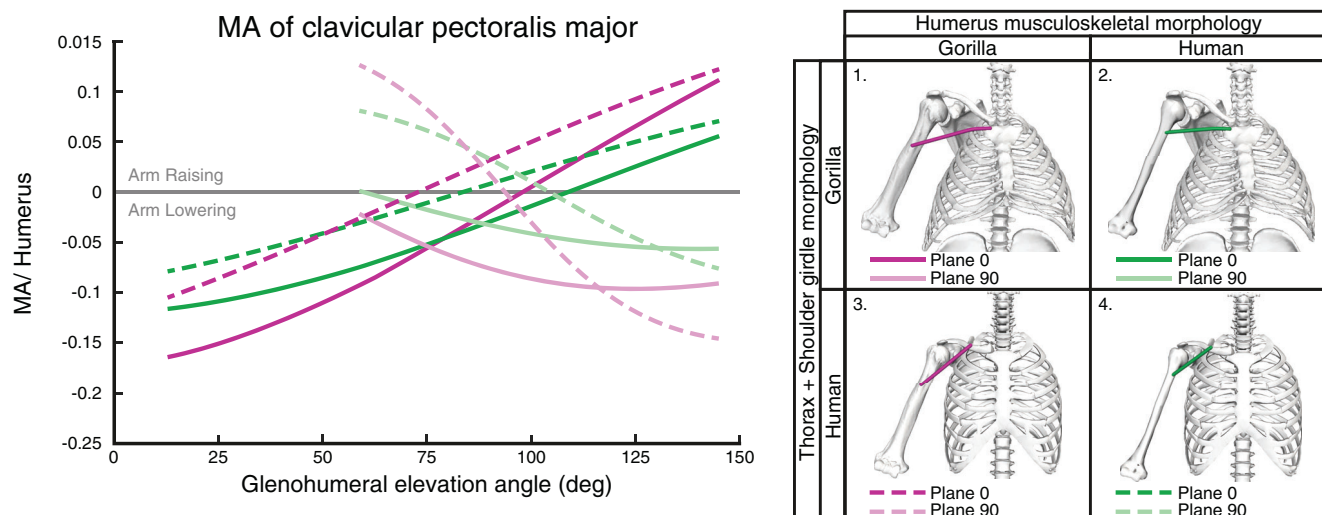


FIGURE 7 Biomechanical consequence of shoulder morphological variation for clavicular pectoralis major. The line style separates the gorilla (solid) from the human (dashed) thorax and shoulder girdle morphology, while the line color separates the gorilla (pink) from the human (green) humerus morphology. MAs estimated in an elevation plane of 0° are in darker color; in an elevation plane of 90° are in lighter color. The model pictures (right side) highlight the different combinations of musculoskeletal morphologies used in the test configurations. MA estimates are normalized by humerus length

The differences in thorax and shoulder girdle musculoskeletal geometry additionally affect the action capability of the clavicular pectoralis major. In the elevation plane of 0° , muscle moment MAs predict a shift from arm-lowering to arm-raising capability in all four configurations (dark pink and dark green curves). However, the elevation angle at which the shift occurs differs; configurations using the gorilla thorax and shoulder girdle musculoskeletal geometry (dark pink solid and dark green solid curves) shift at higher elevation angles. In the elevation plane of 90° , the configurations using the human thorax and shoulder girdle morphology (light pink dashed and light green dashed curves) predict a shift from arm-raising to arm-lowering capability, whereas the configurations using the gorilla thorax and shoulder girdle morphology predict a pure arm-lowering action capability (light pink solid and light green solid curves). Therefore, those configurations using the gorilla thorax and shoulder girdle musculoskeletal geometry exhibit a greater range of glenohumeral elevation angles where the muscle is able to act as an arm-lowering muscle, thereby enhancing its arm-lowering capability.

Humerus morphology and muscle insertion location have a lesser, though still notable effect on clavicular pectoralis major MA. Comparison of the pink solid to the green solid curves shows that altering the gorilla model by substituting the human humerus with its proximal muscle insertion reduces MA. Comparison of the dashed MA curves illustrates the inverse: altering the original human model (green dashed curves) by substituting the gorilla humerus and muscle insertion (pink dashed curves) increases arm-lowering MA in the elevation plane of 90° . In the elevation plane of 0° , the effect is less pronounced.

In summary, the aspect of skeletal architecture that is primarily responsible for the arm-lowering enhancement of clavicular pectoralis major in the gorilla compared to the human model relates to the position of the scapula on the thorax, the orientation of the glenoid and the

location of muscle origin. With the gorilla thorax and shoulder girdle morphology, the GHJ is located well above the manubrium and therefore muscle origin, so the muscle path runs inferior to the GHJ center throughout most tested joint angles and the more negative, larger MAs result. With the human thorax and shoulder girdle, the GHJ is located roughly at the level of the sternum. As the muscle origin is largely located on the clavicle, the differences in spatial relationship result in a muscle origin that is situated superiorly relative to the GHJ, contrarily to the inferior muscle origin position in the gorilla. Thus, the muscle acts as an arm-raising muscle at arm elevation angles below horizontal in the plane of 90° . The arm-lowering capability of the clavicular pectoralis major in gorilla is further enhanced by the more distal muscle insertion on the humerus.

4 | DISCUSSION

In this study, we assessed whether and to what extent gorilla-specific musculoskeletal anatomy enhances the arm-lowering mechanism compared to humans. We found strong support for an enhanced arm-lowering capability in *Gorilla* compared to *Homo*. This enhancement was evident in greater arm-lowering MAs and moment-generating capacities of two important arm-lowering muscles, pectoralis major and teres major. We found no enhancement of arm-lowering capacity in subscapularis and teres minor.

4.1 | The components of an enhanced arm-lowering mechanism

The overall enhanced arm-lowering capacity of pectoralis major and teres major results from both enhanced soft tissue properties and a

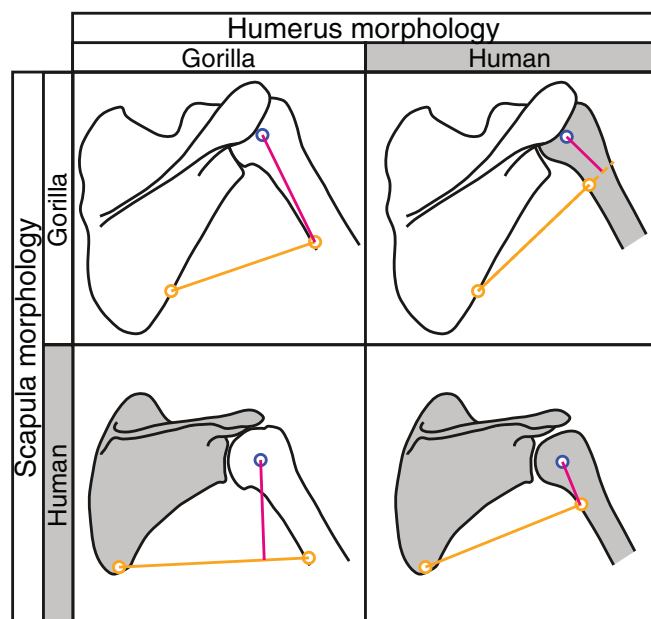


FIGURE 8 Effects of different musculoskeletal features on teres major MA. *Gorilla* skeletal morphology is in white, *homo* skeletal morphology in gray. GHJ center is highlighted using a blue circle. Teres major muscle path (orange) is the linear connection between muscle attachment points (orange circle). The perpendicular distance between GHJ center and muscle path (approximating the MA) is highlighted in pink. Humerus morphology was isometrically scaled to the corresponding scapula morphology

beneficial musculoskeletal anatomy in *Gorilla* compared to *Homo*. The enhanced muscle soft tissue properties provide *Gorilla* with comparatively greater F_{max} values. The magnitude of difference between humans and gorillas was much greater in these arm-lowering muscles than in our previous study that investigated between-species differences in glenohumeral abductors (van Beesel et al., 2021). Therefore, these findings suggest that force-generating capacity across arm-lowering, rather than arm-raising, is enhanced in *Gorilla* compared to *Homo*.

The MA enhancement results from species-specific differences in musculoskeletal anatomy. Based on the results of the test configurations, we created two figures to visually summarize our findings on how musculoskeletal geometry affects the biomechanical performance of teres major and pectoralis major (Figure 8 and Figure 9). Muscle insertion positions and distal limb morphology had the greatest effect on MA, as similarly observed in chimpanzee hindlimb muscles (O'Neill et al., 2013). The more distal muscle insertions on the humerus, which are observed in the gorilla, have the greatest effect on arm-lowering MA enhancement of teres major and sternocostal pectoralis major (Figure 8 and Figure 9, row-wise). *Gorilla* teres major and clavicular portion of pectoralis major MAs are further enhanced by the oblique shoulder morphology in *Gorilla*, but the effect on teres major MA is smaller compared to differences in humerus insertion. The cranially oriented glenoid shifts the location of the GHJ center superiorly relative to the muscle origin, which, in combination with a gorilla-like humerus morphology, further increases the arm-lowering MA (Figure 8 and Figure 9, left column). This biomechanically enhancing effect of gorilla-like oblique shoulder morphology on teres major and

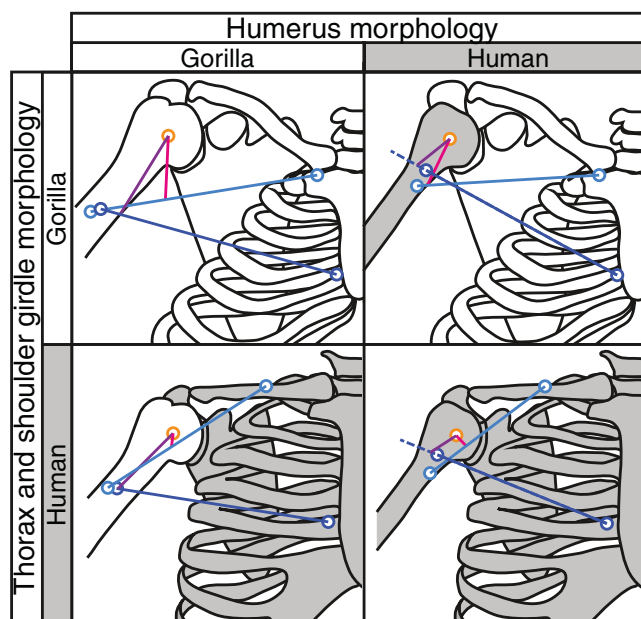


FIGURE 9 Effects of different musculoskeletal features on pectoralis major MA. *Gorilla* skeletal morphology is in white, *homo* skeletal morphology in gray. GHJ center is highlighted using an orange circle. Clavicularis (light blue) and sternocostalis (dark blue) pectoralis major muscle paths are the linear connections between muscle attachment points (blue circles). The perpendicular distance between GHJ center and muscle path (approximating the MA) is highlighted in pink (clavicularis) or violet (sternocostalis). Humerus morphology was isometrically scaled to the corresponding thorax and shoulder girdle morphology

clavicular pectoralis major might somewhat trade-off the decreasing effect observed in sternocostal pectoralis major. Furthermore, the inferior muscle origin relative to GHJ position results in a more lateral fiber orientation of the clavicular portion of pectoralis major, in contrast to what is observed in humans (Ashton & Oxnard, 1963), and enables this MTSU to act as an arm-lowering muscle over a greater range of arm elevation angles (Figure 9, column-wise). A similar consequence of the more oblique shoulder configuration was observed in the clavicular and spinal portions of the deltoid muscle (van Beesel et al., 2021). In summary, our findings support our proposal that *Gorilla*-specific shoulder morphology as well as muscle architectural properties enhance the arm-lowering mechanism compared to *Homo*.

Our results highlight that a combination of traits causes the arm-lowering enhancement that was observed in *Gorilla* compared to *Homo*. While specific traits like a more distal insertion on the humerus might be indicative for an arm-lowering enhancement, the case of the clavicular pectoralis major highlights that none of the traits are responsible or indicative on their own, but only in conjunction. These findings were demonstrated using specimen-specific models, but our investigations highlight specific aspects of musculoskeletal structure that generated those functional differences. Thus, it may be possible to extrapolate these principles to other apes sharing aspects of the gorilla musculoskeletal structure used in this study, though further research in this direction is needed.

Our results are in agreement with the observations of previous studies on nonhuman apes. Intraspecific comparisons of force-production capacities and MA show that the glenohumeral arm-lowering muscles are stronger than the arm-raising muscles (Ashton & Oxnard, 1963; Ashton & Oxnard, 1964; Michilsens et al., 2009; Michilsens et al., 2010; Napier, 1963; Oxnard, 1963; Oxnard, 1967). The magnitude of force-production capacities in nonhuman apes reported here and by previous studies is considerably higher than those in humans, which demonstrates a general enhancement of arm-lowering muscle soft tissue properties. A more distal teres major and pectoralis major insertion along the humerus, which is the main cause of greater arm-lowering MAs between gorillas and humans, was similarly observed in other African apes as well as in arboreal quadrupeds and climbers (Fleagle & Simons, 1982; Stewart, 1936). Again, our findings suggest that humans fall outside of this range, indicating that the arm-lowering mechanism is mechanically enhanced in African apes and possibly all hominoids except humans.

Unfortunately, we were unable to include latissimus dorsi, an important arm-lowering muscle, in our biomechanical analysis. Yet, since this muscle is enlarged in nonhuman apes and its humeral insertion is known to fuse with that of teres major, we expect that this muscle is similarly enhanced in nonhuman apes and displays a relatively more distal insertion position compared to humans.

Currently available comparative data that quantify muscle insertion positions on the humerus focus on differences in deltoid insertion site. This is perhaps a result of the historical focus on the arm-raising mechanism. Only a small number of observations are available for differences in teres major, pectoralis major and latissimus dorsi insertion sites (Ashton & Oxnard, 1963; Fleagle & Simons, 1982; Inman et al., 1944; Stewart, 1936). Our results suggest that future studies investigating the morphological variation of extant and fossil hominoid shoulders would benefit from incorporating more observations on differences in the relative insertion positions of the main arm-lowering muscles. Indeed, this rarely discussed aspect of humerus morphology appears to have a larger impact on shoulder biomechanics than does oblique shoulder morphology, which has received extensive discussion in primate paleontology (Melillo, 2016; Melillo et al., 2019).

Overall, the findings of our biomechanical analysis together with musculoskeletal data reported by previous studies suggest that the arm-lowering mechanism is enhanced in all hominoids except humans. The evidence of an enhanced arm-lowering mechanism could signal an adaptation to locomotor behavior that is shared by all nonhuman apes. We further suggest that the lack of the enhanced arm-lowering mechanism in humans, as reflected by a proximal shift in muscle insertion sites on the humerus, may be related to the fact that the upper limb does not play a role in body propulsion.

4.2 | Importance of arm-lowering-mechanism for gorilla locomotion

Although arm-raising adaptations have been historically emphasized, arm-lowering is clearly an important mechanism in the propulsive phases of ape locomotion (Hunt, 2016; Larson & Stern, 2007). In

vertical climbing and suspensory locomotion, arm retraction is used to elevate the body center of mass (Hunt, 2016). Our results show that the *Gorilla* pectoralis major and teres major arm-lowering capability is enhanced compared to nonarboreal *Homo*. Therefore, our modeling results suggest that gorilla anatomy provides a biomechanical advantage in arboreal locomotor behaviors.

EMG studies of nonhuman apes during vertical climbing show that the arm-lowering muscles are active during these behaviors (Larson & Stern, 1986; Stern et al., 1980). Pectoralis major activity is highest in the beginning of support phase (Stern et al., 1980) when the arm is highly elevated (Isler, 2005). Here, we showed that high glenohumeral elevation angles coincide with maximal moment-generating capacity. Teres major is highly activated during mid-support phase (Larson & Stern, 1986) when the arm is somewhat lowered (Isler, 2005), which coincides with our finding that teres major moment-generating capacity is greater in smaller elevation angles. Therefore, the results of our analysis, in conjunction with kinematic and EMG studies, show that muscles are being recruited during locomotor sequences that require high force generation (i.e. where center of mass is located far below the supporting limb and upward body propulsion is occurring) and that coincide with joint positions where muscle capacity is biomechanically near-optimized. The combined evidence of high-muscle activity and high moment-generating capacity together with an arm-lowering action prediction based on MA suggest a functionally enhanced arm-lowering mechanism that is beneficial in an arboreal context.

In quadrupedal walking, arm retraction is thought to be used to pull the body over the supporting limb during stance phase (Smith & Savage, 2008). Indeed, arm retraction muscles like latissimus dorsi, teres major and pectoralis major were found to be active during these phases in cats and dogs (Nomura, 1966; Tokuriki, 1973; English, 1978). Our MA and moment results predict that teres major is an effective arm retractor (arm-lowering in elevation plane 90°) whereas pectoralis major is an effective arm adductor (arm-lowering in elevation plane 0°) at small glenohumeral elevation angles that potentially coincide with the shoulder angle range observed during knuckle walking (Pontzer et al., 2014). EMG studies on chimpanzees found that teres major is inactive, whereas pectoralis major is active during the support phase (Larson & Stern, 1987; Larson & Stern, 2007). The combined evidence of action capability and muscle activity suggests that pectoralis major functions as an arm adductor rather than as a retractor during quadrupedal stance phase, which confirms the conclusion of Larson and Stern (2007). Furthermore, the high teres major retraction capability in combination with evidence of its inactivity during quadrupedal walking indicate that this locomotor behavior does not require that the shoulder muscles generate as much force compared to vertical climbing.

In summary, an enhanced arm-lowering mechanism is particularly beneficial for ape arboreal locomotor behavior. This strong mechanism is essential for movements that include upward body propulsion with the arm-raised above the head. Therefore, an enhanced arm-lowering mechanism, evident by distal humerus insertions and an oblique shoulder configuration, appear to be indicative for the

orthograde arboreal locomotion of nonhuman apes, and potentially other suspensory species. Parsimony-based reasoning suggests that these traits were lost over the course of hominin evolution.

4.3 | Study limitations

Our gorilla model is specimen-specific, which fits our study design as the model reflects the biomechanical capabilities of an actual animal. However, this approach also has its limitations that can affect the interpretation of the results. A specimen-specific model does not reflect the intraspecific variability present in a species. We approached this limitation by comparing our calculated and reconstructed muscle soft-tissue properties and musculoskeletal geometries to data reported by other studies (Supporting Information section 1). The evaluation suggests that our gorilla model parameters lie within the range observed in African nonhuman apes. The results increase our confidence in the placement of muscle attachment points and the reconstruction of the general morphological pattern found in *Gorilla*. Furthermore, our gorilla F_{\max} values fall at the lower range of values observed in nonhuman apes. Therefore, our results suggest that the F_{\max} differences observed between the human and gorilla model are not the result of an unrepresentatively powerful gorilla specimen.

In this study, we investigated the arm-lowering effectiveness across varying glenohumeral elevation angles and planes. The results highlight that arm-lowering capacity of teres minor and subscapularis is similar between gorillas and humans. However, arm retraction or adduction are not necessarily the main function of these muscles. Teres minor is thought to act as a lateral rotator in nonhuman apes (Larson, 1993). The subscapularis muscle is understood to act as a strong medial rotator that is highly active during vertical climbing (Arias-Martorell, 2018; Larson, 1993; Larson & Stern, 1986). The difference in subscapularis F_{\max} capacity further suggests that this muscle serves different roles in humans and nonhuman apes. Therefore, future biomechanical studies investigating differences in shoulder muscle function within hominoids would benefit from incorporating rotations about the humeral long-axis.

Our biomechanical analysis is focused on mechanisms that act at the GHJ. However, the shoulder complex includes three additional joints (scapulothoracic, sternoclavicular and acromioclavicular). In humans, glenohumeral elevation contributes 120° to a full 180° arm-raise; the remaining excursion is achieved through combined rotations about the other three joints. (Inman et al., 1944; Lucas, 1973). However, it is debated whether and to what extent nonhuman apes employ this mechanism (Larson, 1993; Larson et al., 1991; Tuttle & Basmajian, 1977). Therefore, we decided to not include scapular rotation as part of the arm-lowering mechanism of our gorilla model. However, the results of our test configurations show that species-specific differences in scapular position and glenoid orientation have an effect on the arm-lowering capability of pectoralis major. Therefore, we would expect that scapulothoracic motion affects the biomechanical capability of this muscle. Future studies that investigate

scapulothoracic range of motion in nonhuman apes will shed more light on the biomechanical consequences for pectoralis major. Furthermore, the humeral head is known to translate relative to the glenoid across arm abduction in humans (Hik & Ackland, 2019; Karduna et al., 1996; Massimini et al., 2012). Yet, as the effect of translations on shoulder muscle MAs in humans and the range of translations in nonhuman apes are unknown, we decided to focus our analysis on glenohumeral rotations. However, the modeling aspect enables the integration of glenohumeral translation and scapular rotation in future versions of the model, which gives opportunity and reason for further development.

5 | CONCLUSION

The arm-lowering mechanism is enhanced in *Gorilla* and potentially all nonhuman apes compared to *Homo*. This enhancement is evident by greater maximum isometric force capacities and MAs of two important arm-lowering muscles, the pectoralis major and teres major. The enhanced MAs result from a more distal humerus insertion and more oblique shoulder configuration, morphological features that are present in *Gorilla* and potentially all other nonhuman apes. These insights cast a new light on the functional implications of the differences in human and nonhuman ape shoulder morphology that have been so thoroughly documented. Namely, that rather than imparting an advantage in arm-raising, the bone shapes and articulated shoulder architecture common to nonhuman hominoids and suspensory monkeys are enhancing the arm-lowering mechanism.

A strong arm-lowering mechanism is advantageous in an arboreal context. An effective mechanism benefits locomotor behaviors that include arm-lowering to propel the body center up- and forward, as in vertical climbing and suspension. Therefore, we would expect to find evidence for an enhanced arm-lowering mechanism similar as described for *Gorilla* in all arboreal hominoids. This enhanced mechanism was lost together with arboreal adaptations as bipedalism evolved in hominins.

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AUTHOR CONTRIBUTIONS

Julia van Beesel: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (equal); methodology (lead); project administration (equal); validation (lead); visualization (lead); writing – original draft (lead). **John Hutchinson:** Data curation (supporting); formal analysis (supporting); methodology (supporting); project administration (supporting); supervision (supporting); validation (supporting); visualization (supporting); writing – original draft (supporting). **Jean-Jacques Hublin:** Conceptualization (supporting); funding acquisition (lead); project administration (supporting); supervision (supporting); writing – original draft (supporting). **Stephanie Melillo:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (equal); methodology (supporting); project administration (equal); supervision (lead); visualization (supporting); writing – original draft (supporting).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are partially available in the article and Supporting Information and are available from the corresponding author upon reasonable request.

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CONCLUSION

The primary aim of this thesis is to evaluate the biomechanical capacity of different shoulder musculoskeletal systems within the Hominoidea. This aim is addressed in two independent studies, which evaluate the biomechanical capacity of the glenohumeral arm-raising and arm-lowering muscles in two morphologically distinct species, *Gorilla* and *Homo*, using musculoskeletal models. As expected, the evaluation highlights that the glenohumeral muscle capacities differ between the two species. However, contrary to earlier ideas that proposed an enhanced arm-raising mechanism in *Gorilla* compared to *Homo*, the results of the biomechanical analysis demonstrate an enhanced arm-lowering mechanism in *Gorilla*. The greater arm-lowering capacity is evident by greater moment-producing capacities of the arm-lowering muscles, which result from advantageous musculoskeletal geometries and greater force-producing capacities.

Consequence of different musculoskeletal geometries

This thesis identified certain musculoskeletal traits that affected the muscle moment arms and were thereby responsible for the enhanced arm-lowering mechanism in *Gorilla* compared to *Homo*. These morphological traits enhance the arm-lowering mechanism by firstly enhancing the magnitude of the moment arms and by secondly enabling a greater number of muscles to act as arm-lowering instead of arm-raising agents. Whilst earlier studies have focused on identifying and discussing differences in scapular morphology (i.e. Larson (1993)), the findings here highlight that humerus morphology had the greatest effect on the magnitude of the glenohumeral muscle moment arms. This finding is in agreement with previous biomechanical studies, which found that muscle moment arms are more sensitive to the attachment site that is closer to the joint rotation centre (Murray *et al.*, 2002; Bates *et al.*, 2012; O'Neill *et al.*, 2013; Goh *et al.*, 2017). As the insertion site of most muscles discussed in this thesis is closer to the joint rotation centre than the origin site, the humerus musculoskeletal morphology has the greatest influence on the magnitudes of the moment arms. Instead, thorax and shoulder girdle musculoskeletal geometry, which provide the origin sites, were found to mainly affect the action capability of the glenohumeral muscles.

Consequence of differences in humerus morphology

The findings of the biomechanical analysis (chapter two) show that humerus musculoskeletal geometry has a distinct effect on two important arm-lowering muscles (teres major and pectoralis major). The moment arms of both muscles are enhanced through more distal muscle insertions in *Gorilla* compared to *Homo*. The more distal muscle insertion causes the muscle path to shift to an inferior position relative to the glenohumeral joint centre, in comparison to the human configuration. This further inferior muscle path results in a greater distance between muscle line of action and glenohumeral joint centre, and thereby in greater moment arms. The distance between muscle insertion position and proximal end of humerus head is expressed as the position index (Schultz, 1918). The position indices of the gorilla and human model together with those reported by two other studies suggest that the distance between the end of the humeral head and muscle insertion of teres major and pectoralis major is greater in the African apes compared to modern humans (Stewart, 1936; Fleagle and Simons, 1982). This would indicate that the adaptation towards an

enhanced arm-lowering mechanism was lost during hominin evolution. Thereby, this thesis identified a mechanically important anatomical trait that has rarely been investigated in previous studies and that will benefit the interpretation of the fossil record. However, this identification is based on the comparison of the musculoskeletal anatomy of two subjects and current comparative datasets are small. Future comparative morphology studies will be able to evaluate whether the observed characteristics are based on true interspecific differences.

Muscle insertion positions along the humerus have traditionally been discussed in relation to enhancing the arm-raising muscles. The main arm-raising muscle, the deltoid, is especially thought to be biomechanically enhanced through the more distal insertion position along the humerus (Schultz, 1918; Inman *et al.*, 1944; Ashton and Oxnard, 1963). Therefore, the greater deltoid position index in suspensory primates is understood as a signal for an enhanced arm-raising mechanism (Inman *et al.*, 1944; Ashton and Oxnard, 1963; Ashton and Oxnard, 1964). However, the results of the biomechanical evaluation (chapter 1) highlight that the acromial deltoid moment arm, the part of the muscle that is mainly involved in arm-raising, is similar in *Gorilla* and *Homo*. Therefore, a more distal deltoid muscle insertion does not enhance the arm-raising moment arm. The results are in agreement with simulations of deltoid muscle elongation in humans, where it was found that the more distal muscle insertion did not affect the deltoid moment arms (De Wilde *et al.*, 2002). The reason for the different effects of a more distal muscle insertion on the deltoid versus the teres major and pectoralis major muscles lies in the deltoid musculoskeletal configuration. As the origin of the acromial deltoid is closer to the glenohumeral joint rotation centre compared to the insertion site, a more distal deltoid insertion position has negligible effects on its path or line of action. Instead, the acromial deltoid moment arm is mainly controlled by the amount of wrapping around the humeral head in both species (see below). As a result, the position index appears to be mechanically meaningful for the glenohumeral arm-lowering muscles, but not for the arm-raising muscles.

However, the biomechanical comparison showed that the *Gorilla*-specific humerus morphology provides an enhancement for the arm-raising capability of the supraspinatus muscle (chapter one). The supraspinatus muscle moment arms are enhanced through a greater lateral protrusion of the greater tubercle, which is the supraspinatus muscle insertion site on the humerus. This greater lateral protrusion increases the distance between muscle line of action and glenohumeral joint centre, which results in the greater moment arms observed in *Gorilla* compared to *Homo*. Furthermore, the maximum isometric force capacity is greater in *Gorilla* compared to *Homo*, which results in overall enhanced supraspinatus muscle moments. The supraspinatus muscle belongs to the rotator cuff and as such mainly acts as a stabilizer of the glenohumeral joint in humans (Gray and Lewis, 1918; Di Giacomo *et al.*, 2008). However, its function within the other apes is still contentious. Whilst researchers conducting EMG experiments suggested that the supraspinatus employs a similar stabilizing role in chimpanzees during quadrupedal walking (Larson and Stern, 1987), its high activity during brachial elevation led to the suggestion that the supraspinatus aids the deltoid during arm-raising (Larson and Stern, 1986). The results of this thesis in conjunction with EMG data suggest that the *Gorilla* supraspinatus muscle would be well suited to support the deltoid muscle over arm-raising. This supporting role might be of greater importance than a stabilizing role, due to the finding that parts of the deltoid muscle have an arm-lowering, rather than an arm-raising action capability. Therefore, the enhancement of the *Gorilla* supraspinatus muscle might be compensating the somewhat reduced arm-raising capacities of the deltoid muscle.

This thesis highlights humerus morphological traits that are indicative for an enhanced arm-lowering mechanism in hominoids. As proximal long bones like the humerus are usually better preserved in the fossil record than delicate skeletal elements like the scapula (Bello and Andrews, 2006), the investigation of these traits in future studies provides an additional new possibility to analyse and reconstruct the musculoskeletal capability of fossil hominoids.

Consequence of differences in thorax and shoulder girdle morphology

Previous proposals suggested that the observed differences in shoulder morphology within Hominoidea enhance the arm-raising mechanism (Keith, 1923; Schultz, 1936a; Schultz, 1936b; Oxnard, 1967; Jenkins *et al.*, 1978; Larson, 1993). This idea is based upon comparative morphology studies that describe a covariation in scapular morphology and locomotor behaviour between arboreal apes and suspensory monkeys (Miller, 1932; Inman *et al.*, 1944; Larson, 1993; Larson, 1995; Young, 2008; Schmidt and Krause, 2011). However, the biomechanical evaluation of the glenohumeral muscles highlights a different interpretation of the long-known differences in thorax and shoulder girdle morphology between *Gorilla* and *Homo*. The results of this thesis suggest that ape-specific thorax and shoulder girdle morphology enhances the arm-lowering capability compared to humans. The *Gorilla* thorax and shoulder girdle morphology was found to mainly affect the muscle action capability. The specific morphological traits change the position of the muscle line of action relative to the glenohumeral joint. As a result, certain muscles (or sections thereof) that act as arm-raising muscles in humans instead act as arm-lowering muscles in gorillas.

An inferior muscle path relative to joint rotation centre translates muscle contraction into a negative humerus rotation and, therefore, results in an arm-lowering action. In *Gorilla*, the cranially oriented glenoid fossa results in more inferiorly positioned origins for the clavicular and spinal deltoid and clavicular pectoralis major relative to the glenohumeral joint centre. As the insertion position is also inferior to the glenohumeral joint, the cranially oriented glenoid fossa results in an inferior muscle path position, and, therefore, in an arm-lowering moment arm. Apart from affecting the position of the glenohumeral joint centre, the *Gorilla* thorax and shoulder girdle morphology further affects the origin position of all three muscles. The obliquely oriented scapular spine found in *Gorilla* and other non-human apes shifts the origin position of the spinal deltoid inferiorly relative to the glenohumeral joint centre (chapter one). This causes a further inferior shift of the whole muscle path relative to the glenohumeral joint centre, which is strikingly different from the human spinal deltoid muscle path that instead, due to the transversely oriented spine, runs close to the glenohumeral joint. The more inferior path position in *Gorilla* enables this muscle to act solely as an arm-lowering muscle, removing the arm-raising action capability that is observed in *Homo*. A similar inferior shift of the origin position relative to glenohumeral joint centre was observed for the clavicular deltoid and clavicular pectoralis major in *Gorilla*. This shift is caused by the obliquely oriented clavicle and the cranial position of the scapula on the thorax. As a result, both muscles are able to act as arm-lowering muscles over a wider range of joint angles in *Gorilla* compared to *Homo*. Furthermore, the origin of the clavicular pectoralis major in *Gorilla* is concentrated on the manubrium, and only a small portion of the clavicle serves as an attachment site (chapter two). As a result, the centroid of the origin site is located on the manubrium, which moves the origin position further inferior relative to joint rotation centre. Therefore, the *Gorilla* origin position is moved further inferior compared to an origin position that is concentrated on the clavicle, as is the case in humans. The inferior position of the muscle paths relative to the glenohumeral joint centre, caused by morphological traits that are understood to signal adaptations to arboreality and suspension, result in a greater range of elevation angles where the muscles are able to act as arm-lowering muscles in *Gorilla* compared to *Homo*. As similar morphological traits are found in other non-human apes (Schultz, 1930; Miller, 1932; Larson, 2007; Larson, 2009; Diogo and Wood, 2012; Larson, 2013), it is likely that these species employ similarly enhanced arm-lowering mechanisms.

Apart from the aforementioned morphological traits of the thorax and shoulder girdle, a greater lateral projection of the acromion is thought to be advantageous for the arm-raising mechanism (Roberts, 1974; Corruccini and Ciochon, 1976; Ciochon and Corruccini, 1977). An acromion with a greater protrusion beyond the glenoid facet, which is observed in arboreal apes but not humans (Ciochon and Corruccini, 1977), is thought to provide a greater leverage for the acromial deltoid. However, the results of the biomechanical analysis (chapter one) reveal that the acromial deltoid moment arm is similar between *Gorilla* and *Homo*. This similarity in moment arms despite the

notable differences in morphology indicates that the degree of acromion projection does not influence the distance between muscle path and glenohumeral joint centre. Studies investigating the biomechanical capability in humans have suggested that the deltoid moment arm is dependent on the wrapping of the muscle path around the humeral head (Howell *et al.*, 1986; Rietveld *et al.*, 1988; Iannotti *et al.*, 1992; Nyffeler *et al.*, 2006). However, in healthy human subjects as well as in the gorilla model specimen, the acromion does not project beyond the lateral extend of the humeral head. Therefore, the lateral extend of the humeral head dictates the wrapping radius and the distance between muscle line of action and joint centre. As a result, the greater lateral acromion projection does not enhance the arm-raising mechanism in *Gorilla* and potentially other non-human apes compared to *Homo*.

Consequence of differences in force-producing capacities

The biomechanical analysis (chapter two) revealed enhanced force-producing capacities of teres major and pectoralis major in *Gorilla* compared to *Homo*. The greater maximum isometric force capacities of both muscles together with the beneficial moment arms result in overall enhanced muscle moment capacities over arm-lowering in *Gorilla*. These findings are in line with the results of other studies that noted similar trends for greater force-producing capacities in the arm-lowering muscles of non-human apes (Ashton and Oxnard, 1963; Napier, 1963; Oxnard, 1963; Ashton and Oxnard, 1964; Oxnard, 1967; Michilsens *et al.*, 2009; Michilsens *et al.*, 2010). Overall, the results indicate that the arm-lowering mechanism in *Gorilla* and potentially other non-human apes is enhanced by both morphological and force capacity properties. The evident enhancement suggests that the arm-lowering mechanism is of significance to the locomotor habits of non-human ape species.

The analysis further revealed that the maximum isometric force capacity of the subscapularis muscle in *Gorilla* exceeds that of *Homo* by twofold when controlled for body size (chapter two). However, the arm-lowering muscle moment capacity is small in *Gorilla* and similar to *Homo*, despite the higher maximum isometric force capacity. This similarity in moment capacity is a result of the smaller subscapularis moment arm in *Gorilla* compared to *Homo*. The evidence of a small arm-lowering moment arm but high force-producing capacity suggests that the main function of this muscle is likely related to a task different from arm-lowering. Apart from being considered as an arm-lowering muscle, EMG studies suggested that this muscle is acting as an internal rotator (Larson and Stern, 1986; Larson, 1993; Arias-Martorell, 2018). However, this thesis did not investigate humeral long-axis rotation capability. Future studies that further investigate the action capability of the subscapularis will shed more light on the potential function of this muscle in non-human apes.

Overall, the force capacities of the arm-raising muscles are similar between the arboreal gorillas and terrestrial humans (chapter one). Therefore, evidence from both musculoskeletal geometry and soft tissue properties suggests that the arm-raising mechanism is not enhanced in *Gorilla* compared to *Homo*. Thus, it is likely that no enhanced arm-raising mechanism is required in gorillas for suspensory or arboreal locomotion. However, the acromial deltoid is able to maintain higher moment capacities in highly elevated arm positions in *Gorilla* compared to *Homo*. This is a result of differences in the deltoid force-length properties between the two species. These differences could stem from a more distal muscle insertion along the humerus in *Gorilla* compared to *Homo*. While the more distal muscle insertion does not enhance the deltoid moment arm, it also results in a muscle that is elongated and able to produce force over a greater range of motion. This is in agreement with a study in humans, which found that the deltoid muscle is able to produce peak forces at higher elevation angles after being elongated (De Wilde *et al.*, 2002). However, muscles with longer muscle fibres tend to produce smaller maximum isometric forces at similar muscle weights (Zajac, 1989). This loss in maximum isometric force capacity is potentially compensated for by the high

supraspinatus maximum isometric force and moment capacity across arm-raising. Therefore, instead of enhancing the arm-raising capacity, the *Gorilla* musculoskeletal system shifts the peak arm-raising moments towards higher elevation angles compared to *Homo*.

The ability to produce peak moments at highly elevated arm positions could suggest that the arm-raising mechanism works differently in gorillas and humans. While in humans up to 120° of a total 180° arm-raise occur at the glenohumeral joint (Codman, 1934; Lucas, 1973; Duprey *et al.*, 2015), this range might be broader in non-human apes. As a result, the proportion of scapular rotation during arm-raising might be reduced in non-human apes compared to humans. Currently, the amount of scapulothoracic rotation during arm-raising in non-human hominoids is highly debated and yet unresolved. Future studies investigating scapular motion will cast further light on scapulothoracic rotation and the arm-raising mechanism in non-human apes.

Importance for locomotor behaviour

The arm-lowering mechanism is essential to the locomotor behaviour of arboreal hominoids. Kinematic studies investigated muscle activity during typical non-human ape locomotor behaviours like quadrupedal walking, vertical climbing and arm-hanging (Stern *et al.*, 1980; Fleagle *et al.*, 1981; Larson and Stern, 1986; Larson and Stern, 1987; Larson and Stern, 2007). These studies found that the arm-lowering muscles like pectoralis major and teres major display the highest activities during the propulsive phases of vertical climbing and suspension, whereas only moderate to no activity was detected during knuckle-walking. During these propulsive phases, the body is elevated by pulling the arm down (Isler, 2005). The high muscle activity suggests that the hoisting behaviours are demanding high muscle force output (Hunt, 2016). Therefore, the generally enhanced arm-lowering mechanism in gorillas and potentially other non-human apes would be beneficial for the hoisting movements during vertical climbing and suspension. This alternate interpretation of the non-human ape musculoskeletal system has been proposed earlier, but was not widely discussed (Michilsens *et al.*, 2009; Michilsens *et al.*, 2010; Hunt, 2016). The results here now add more evidence and support to the reasoning.

To conclude, this thesis evaluated the biomechanical consequences of two distinct thorax and shoulder girdle musculoskeletal morphologies within the Hominoidea. The results highlight morphological traits that are of potential biomechanical significance for the arboreal locomotor habits of non-human apes. As such, the results of this thesis enable future comparative morphology studies to focus on biomechanical important musculoskeletal traits. Furthermore, this thesis provides a better understanding of the link between the conformation of a morphological trait and its biomechanical capability. A better understanding of this link is essential for the functional interpretation of shoulder morphology. By this, the thesis adds towards the interpretational foundation that is required to evaluate the biomechanical capability of extinct species, such as the intermediate shoulder morphology that is observed in *Australopithecus* (Melillo, 2016).

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Appendix A

Supplementary Information for Chapter 1

Published article:

van Beesel J, Hutchinson JR, Hublin J-J, Melillo SM (2021) Exploring the functional morphology of the *Gorilla* shoulder through musculoskeletal modelling. *Journal of Anatomy*, **239**(1), 207-227.

Electronic Supporting Information

SI Text S1. Sensitivity analysis

Positions of muscle attachment influence muscle paths, and therefore muscle moment arms. In order to compare muscle moment arm results of the gorilla model from this study and the human model of Seth *et al.* (2019), we modelled attachments similar to the human model, while still reflecting MTU geometry captured during the gorilla dissection. However, supra- and infraspinatus are each separated into two subunits in the human model, but only modelled as one in the gorilla model (Table 1). While insertion points of both subunits are similar for each muscle, the distance between origin positions is marked. We therefore altered the origin points of both supra- and infraspinatus in the here presented gorilla musculoskeletal model to replicate the positions in the human model. The results of the sensitivity analysis are presented in SI Figure 2 for supraspinatus and in SI Figure 3 for infraspinatus.

SI Text S2. MTU geometry reconstruction

Muscle attachments: While taking muscles off during the dissection, the circumference of each muscle-tendon unit (MTU) was labelled using coloured pins (SI Figure 4) on all bones they were attached to. Additionally, different coloured pins were used to label anatomical landmarks previously identified. Photographs were taken for later reference. Surface scans, using a structured-light surface scanner (Artec Space Spider with Artec Studio 12 software, Artec 3D, Luxembourg), were taken for attachment areas of each MTU, with both origin and insertion sites in one scan. Multiple scans were taken (e.g. overview and detail scans) and fused into one surface using the scanning software (Artec Studio 12 software, Artec 3D, Luxembourg). In Avizo software (version 9.3.0, Visualization Sciences Group, Burlington, MA, USA), the labelled anatomical landmarks were used for a landmark-based affine registration of the scan surface to the bone surfaces of the CT scan. Here, each surface scan was registered to the space of each bone containing attachment areas (in the example of SI Figure 4, the acromial and spinal deltoid surface scan was duplicated and one registered to the scapula surface, one registered to the humerus surface). In Geomagic Studio® (version 2013, RSI 3D-Systems), the surface scans were made transparent and the pins on the surface scans surrounding the muscle attachment areas were used to label these areas on the bone surfaces. The attachment areas were extracted from the bone surfaces and the centroids were calculated in Rhinoceros software (version 6, McNeel Europe, Spain).

Muscle paths: Before taking the muscles off during the dissection, the midline of each MTU was labelled as well as anatomical landmarks using coloured pins (SI Figure 5 A). Photographs were taken for later reference. Surface scans were taken for three different arm positions (abducted, intermediate and adducted). For each arm position, a surface was created in the scanning software. The surface was then registered to the bone surface the captured MTU was originating from (SI Figure 5 B; all muscles were registered to the scapula surface, except the clavicular deltoid, which was registered to the clavicle surface) in Avizo software. The registered path surfaces were imported into OpenSim and previously calculated muscle attachments were inserted into the model. Specific path points and wrapping surfaces used in the human model of Seth *et al.* (2019) were inserted. The resulting MTU paths were evaluated using the labelled midline visible in the path surfaces (SI Figure 5 C) for the three different arm positions. Path points and wrapping surfaces were adjusted to restrict path points to the labelled midlines.

SI Text S3. Comparison of MTU properties

The comparison of MTU properties measured in this study is difficult due to a lack of data reported for female gorillas. Females are not miniature males, as the segment masses relative to body mass differ between sexes (Zihlman, 1992). Zihlman and McFarland (2000) found that male gorillas have relatively heavier forelimbs compared to females. Moreover, the deltoid muscle was found to be lighter in females relative to total muscle mass compared to male gorillas. Therefore, we expect muscle masses relative to body mass to be smaller for female than male gorillas. Muscle fascicle length would be expected to relate to segment length (which might not scale with body mass). However, this data is usually not reported. Therefore, muscle fascicle length and PCSA (based on both muscle mass and fascicle length) are compared relative to body mass. Unfortunately, Kikuchi and Kuraoka (2014) did not report the body mass of their gorilla specimen, but MTU property data is similar to data reported by Payne (2001), with the exception of deltoid fascicle length and PCSA (SI Table 2).

Muscle masses relative to body mass are smaller in the female than the male gorilla (Payne, 2001) as expected, as well as relative PCSA values (SI Table 2). However, relative fascicle lengths are greater in the female gorilla, with a pronounced difference between deltoid fascicle lengths. This could be a result of relatively bigger segments (shoulder and upper arm), or of an overestimation of fascicle length of the female gorilla. Additionally, both studies that report MTU properties of gorillas do not give details where fascicle length data was collected across the deltoid muscle. As fascicle lengths differ highly between the acromial and the other two deltoid MTUs (Table 3), the knowledge about sample position is crucial for comparison. If only relative fascicle length of the acromial deltoid MTU is compared to data reported by Payne (2001), differences are less pronounced. However, as longer fascicle lengths lead to smaller PCSA and maximum isometric force values, an overestimation of force and moment capacity for the gorilla model is unlikely.

We additionally included MTU property data of *Pan troglodytes* into SI Table 2 for comparison. However, it is important to bear in mind that geometrical relationships do not scale with size in African apes. Species with increased body size become relatively shorter and more stout, which might result in smaller MTU properties relative to body mass (see Isler (2005) and references therein). Indeed, relative MTU properties are smaller in the female gorilla compared to the data reported by the other studies (with four exceptions, labelled by an asterisk in SI Table 2). Deltoid and supraspinatus muscles masses reported by Carlson (2006) are relatively smaller compared to the female gorilla (relative masses of infraspinatus are nearly identical). The differences could be related to the high age of the *Pan* specimen, and therefore age related loss of muscle masses. Similarly, relative muscle fascicle lengths of supra- and infraspinatus are shorter in that specimen, but not of deltoid.

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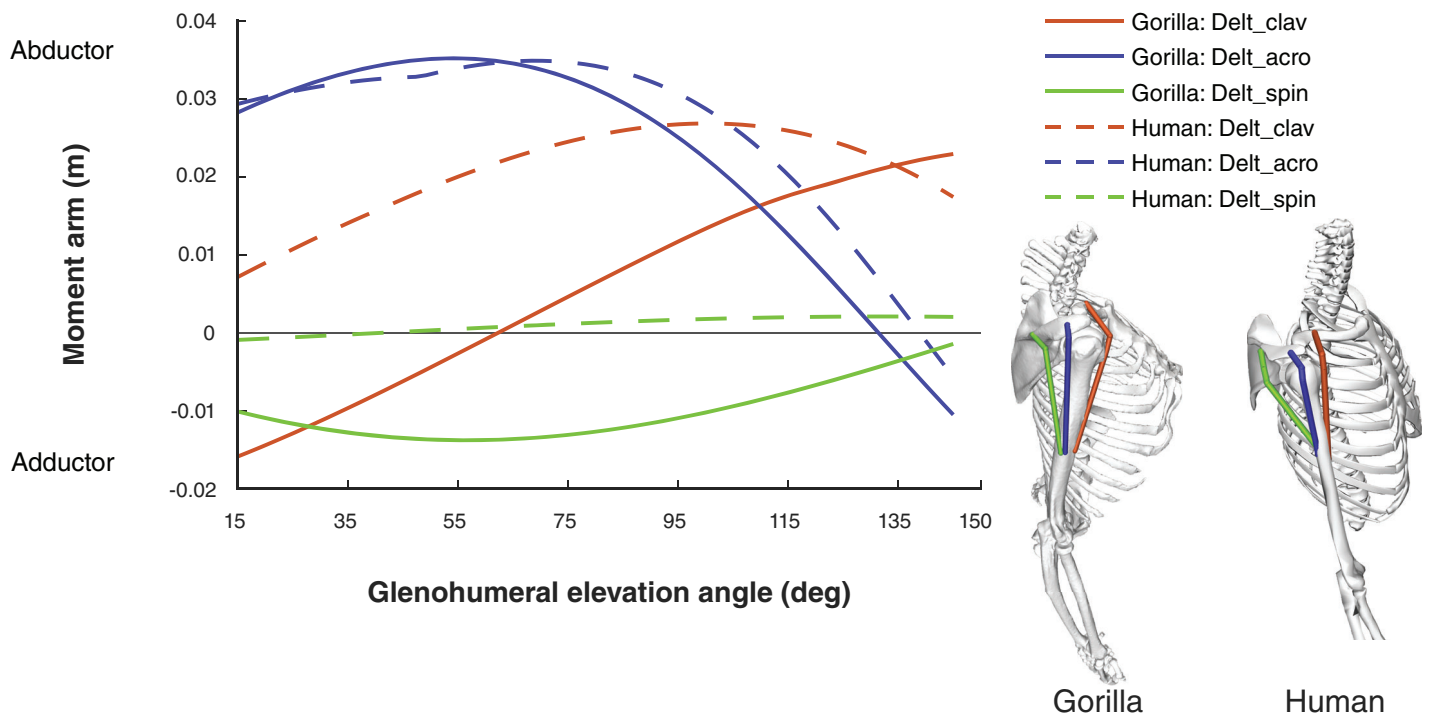
Supporting information tables

SI Table 1. Recalculation of maximum isometric force values used in the human model. Soft tissue property values published by Klein Breteler *et al.* (1999) were used to recalculate F_{max} values. Calculations were based on Hutchinson *et al.* (2015) as described in Materials and Methods.

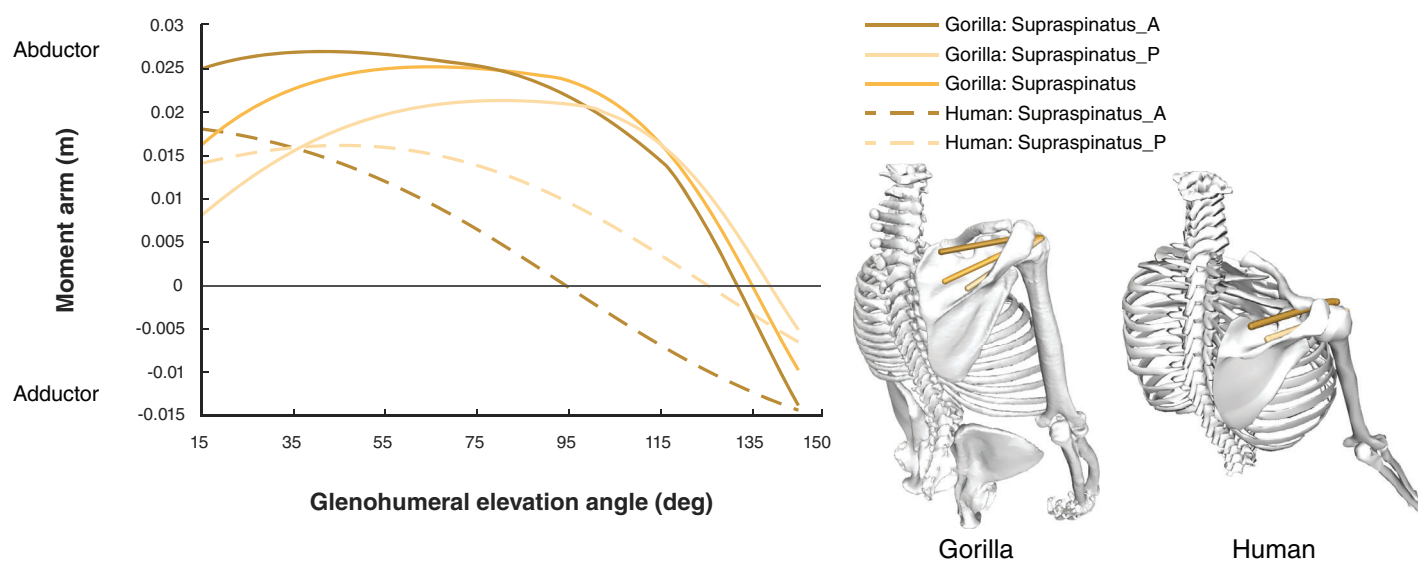
Muscle unit full name	Muscle-tendon unit (model) abbreviation	Maximum isometric force; F_{max} (N)
Deltoideus pars clavicularis	DeltoideusClavicle_A	161.52
Deltoideus pars acromialis	DeltoideusScapula_M	595.03
Deltoideus pars spinalis	DeltoideusScapula_P	302.60
Supraspinatus anterior	Supraspinatus_A	124.69
Supraspinatus posterior	Supraspinatus_P	74.92
Infraspinatus superior	Infraspinatus_S	223.27
Infraspinatus inferior	Infraspinatus_I	238.25

SI Table 2. Comparative MTU properties of deltoid, supraspinatus and infraspinatus reported in this study and in the literature. If data of multiple specimens was reported, only the specimen with the most complete data or best compatibility (based on body weight, age and sex) is represented here. The asterisk labels MTU property values that are smaller relative to body mass compared to MTU properties reported in our study.

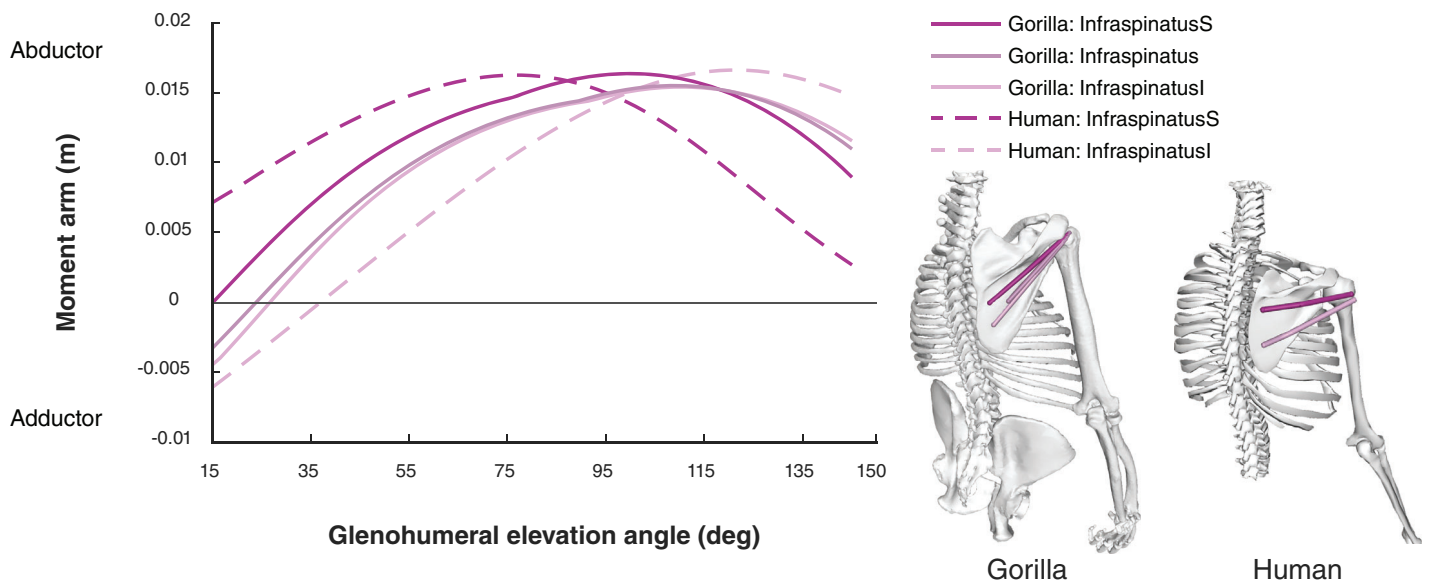
Study	Species	Body mass (kg)	Sex	Age	Muscle	Muscle mass (kg)	Fascicle length (m)	PCSA (m ²)
This study	<i>Gorilla gorilla</i>	80	Female	49	Deltoideus	0.2862	0.1335 (average)	0.0020 (average)
					Supraspinatus	0.0840	0.0662	0.0012
					Infraspinatus	0.1048	0.0839	0.0012
Kikuchi and Kuraoka (2014)	<i>Gorilla gorilla</i>	-	Male	-	Deltoideus	0.680	0.0969	0.0066
					Supraspinatus	0.172	0.0804	0.0020
					Infraspinatus	0.2798	0.1098	0.0024
Payne (2001)	<i>Gorilla gorilla</i>	130	Male	35	Deltoideus	0.6008	0.0631*	0.008979
					Infraspinatus	0.2677	0.1137*	0.00222
Carlson (2006)	<i>Pan troglodytes</i>	54.7	Female	48	Deltoideus	0.1727* (wet)	0.094	0.00174
					Supraspinatus	0.0382*	0.02*	0.00177
					Infraspinatus	0.0742	0.042*	0.00167 (wet)
Kikuchi et al. (2012)	<i>Pan troglodytes</i>	32.2	Female	Adult	Deltoideus	0.18088	0.0543	0.0030
					Supraspinatus	0.0338	0.0406	0.0007
					Infraspinatus	0.06243	0.0598	0.0009
Oishi et al. (2009)	<i>Pan troglodytes</i>	30.2	Female	11	Deltoideus	0.2054	0.0867	0.0022
					Supraspinatus	0.0526	0.038	0.0013
					Infraspinatus	0.1103	0.064	0.0016
Thorpe et al. (1999)	<i>Pan troglodytes</i>	37	Male	6	Deltoideus	0.276	0.083	0.0031
					Infraspinatus	0.116	0.068	0.0016



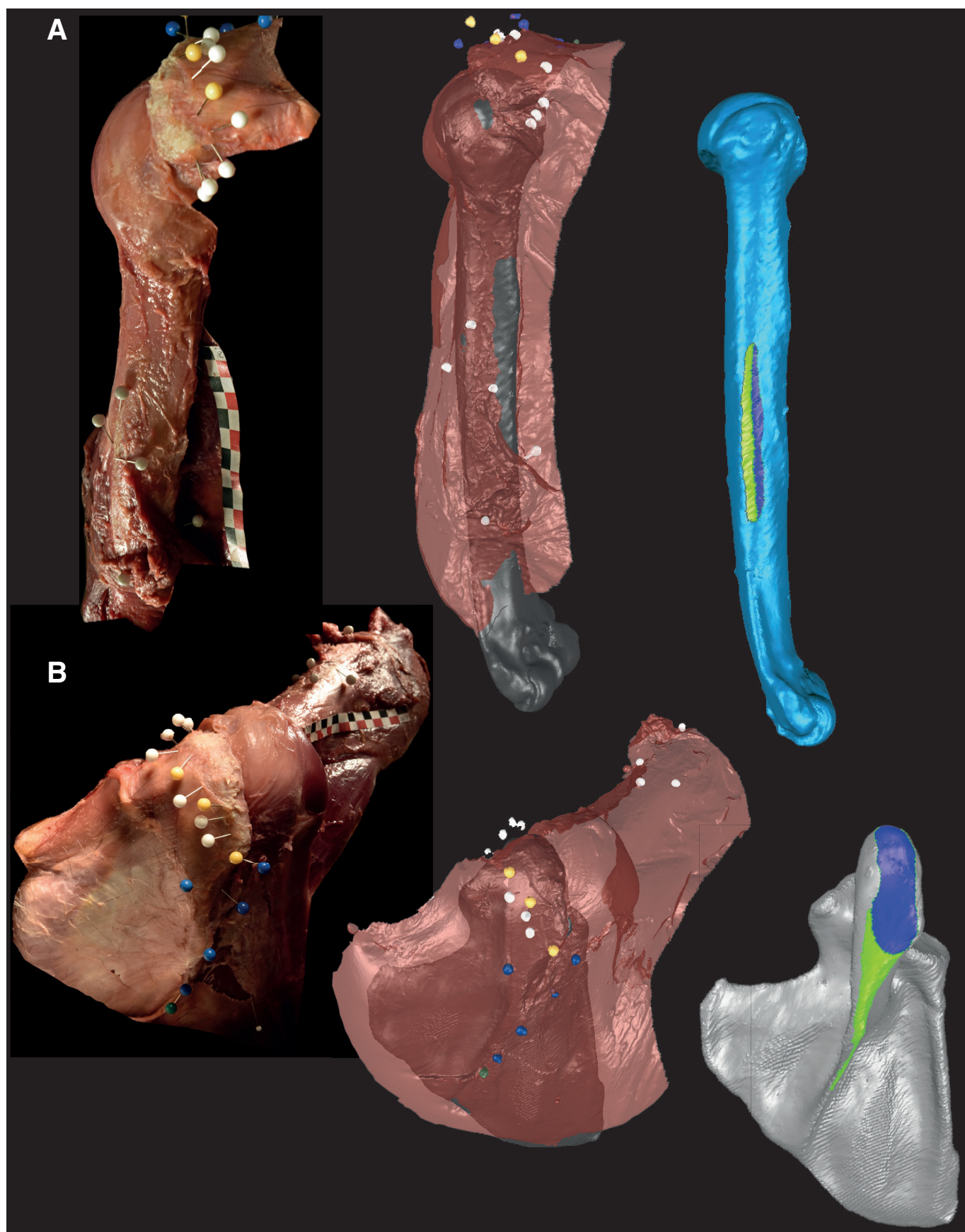
SI Figure 1. Absolute moment arm changes of deltoid muscle over glenohumeral elevation. The grey solid line separates MTUs acting as abductors (positive moment arms) from those acting as adductors (negative moment arms).



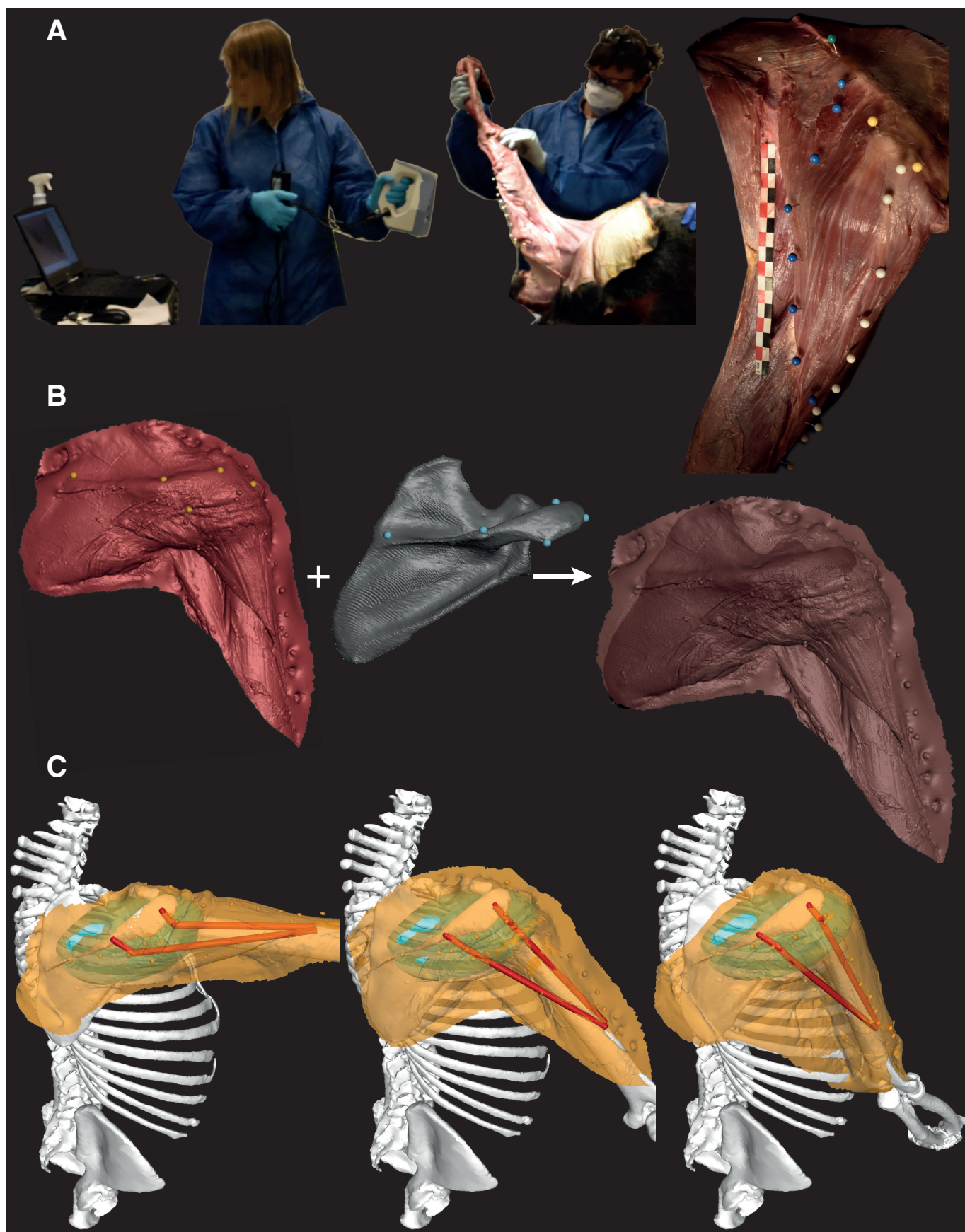
SI Figure 2. Sensitivity analysis of supraspinatus absolute moment arms. Supraspinatus muscle is represented by two subunits in the human model, with differing scapular attachments. Similar muscle origin positions of both subunits were remodelled in the gorilla model to analyse the influence on moment arm. For muscle abbreviations see SI Table 1. The grey solid line separates muscle units acting as abductors (positive moment arms) from those acting as adductors (negative moment arms).



SI Figure 3. Sensitivity analysis of infraspinatus absolute moment arms. Infraspinatus muscle is represented by two subunits in the human model, with differing scapular attachments. Similar muscle origin positions of both subunits were remodelled in the gorilla model to analyse the influence on moment arm. For muscle abbreviations see SI Table 1. The grey solid line separates muscle units acting as abductors (positive moment arms) from those acting as adductors (negative moment arms).



SI Figure 4. Reconstruction of acromial and spinal deltoid attachment surfaces on the humerus (A) and scapula (B). Left: Photographs taken to highlight the position of different coloured pins on the bone and to help reconstructing the surface scans. White pins label attachment area of both MTUs on the humerus and of acromial deltoid on the scapula, blue pins label spinal deltoid attachment area on the scapula. Yellow and green pins label anatomical landmarks. Middle: Registration of surface scan (red) to bone surface from CT (dark grey) based on anatomical landmarks. Right: Attachment areas of spinal deltoid (green) and acromial deltoid (blue) on the humerus and scapula.



SI Figure 5. Muscle path reconstruction of the acromial and spinal deltoid. A. Surface scans were taken for three different arm positions (adducted, intermediate and abducted). Coloured pins label the midline of acromial (white pins) and spinal (blue pins) deltoid, whereas yellow pins label anatomical landmarks. B. Anatomical landmarks were applied to the surface scan (left) and bone surface of CT scan (middle) and used to register the surface to the CT scan (right). C. Registered surface scans (orange) were inserted into the musculoskeletal model and the glenohumeral joint was manipulated to mirror the arm positions of the three different surface scans (abducted, left; intermediate, middle; adducted, right). Pins labelling the midline of each MTU (red) were visible and aided in evaluating muscle paths and assessing the wrapping surfaces (blue)

Appendix B

Supplementary Information for Chapter 2

Published article:

van Beesel J, Hutchinson JR, Hublin J-J, Melillo SM (2022) Comparison of the arm-lowering performance between *Gorilla* and *Homo*. *American Journal of Biological Anthropology*.

Comparison of the arm-lowering performance between *Gorilla* and *Homo* through musculoskeletal modeling – Supporting Information

Supporting Information 1 – MTU reconstruction in the gorilla model

MTU geometry

Muscle attachment locations and paths used in the gorilla model were determined by combining the bone meshes with data acquired during the dissection. We used colored dissection pins to label the midline of each MTU and of osteological landmarks on the scapula and thorax midline. These pins allowed us to track the relevant aspects of musculoskeletal geometry (e.g. change in muscle paths), as we passively manipulated the glenohumeral joint. We captured this information using a structured-light surface scanner (Artec Space Spider with Artec Studio 12 software, Artec 3D), which generated a virtual three-dimensional surface model. Subsequently, the muscles were taken off and the circumference of their attachment sites, along with osteological landmarks, were labeled using dissection pins. This arrangement was again digitized using the surface scanner.

Each three-dimensional surface scan was registered to the corresponding CT bone mesh. The osteological landmarks were used for the affine registration, performed in Avizo software (version 9.3.0, Visualization Sciences Group). In Geomagic Studio®, the dissection pins captured by the surface scan were used to extract each muscle attachment surface from the CT bone mesh (see Figure 1). The centroid of each attachment surface, which was used as muscle attachment point in the OpenSim model, was calculated in Rhinoceros software (version 6, Mc Neel Europe).

In OpenSim, wrapping surfaces and path points constrain muscle paths. The editing of muscle paths followed a twofold approach: first, wrapping surfaces similar to those used in the human model were introduced, to maximize comparability between the two models. Second, the resulting muscle paths were evaluated by introducing the surface scans that capture the muscle paths in different arm positions into the model space in OpenSim. The existing wrapping surfaces were altered or new wrapping surfaces were added, so that the modeled muscle paths followed the dissection observations (i.e., the labeled muscle midlines captured by the surface scans; see Figure 1). The wrapping surfaces used in the gorilla model are reported in Table S 1.

Evaluation of musculoskeletal geometry

In order to evaluate the musculoskeletal geometry of our model, we compare the attachment sites identified in dissection to previously published data. Schultz (1918) developed a position index that quantifies the degree of distal muscle insertion relative to bone length.

The position index of Schultz (1918) is calculated following Stewart (1936):

$$\text{Position index} = \frac{\text{Distance of midpoint of muscle attachment from proximal end of humerus} \times 100}{\text{Maximum length of humerus}}$$

The distance of muscle attachment to humerus head was estimated using Rhinoceros software. We created transverse planes at the muscle attachment point and at the proximal end of the humerus. Both planes were connected by an orthogonal line and the length of the line was calculated (Figure S 1). This distance was measured for all arm-lowering muscles in both the human and gorilla models. The humerus length is 0.359 m in the gorilla and 0.326 m in the human model.

The position indices calculated in both models, together with comparative data reported by previous studies, are presented in Table S 2. A high position index indicates that the muscle insertion point sits

more distally on the humerus. Our gorilla specimen has the highest indices of all muscles except teres minor. The teres major index is similar to that reported for chimpanzees (Fleagle and Simons, 1982). The gorilla model pectoralis major index is higher than those reported for an infant gorilla and a young chimpanzee specimen (Stewart, 1936). However, both individuals were very young. As the distance of muscle attachment to end of humerus might be affected by long bone growth, which originates from the epiphyseal plates, it is possible that the position index changes during ontogeny. Therefore, we expect that the geometry data of our female gorilla lies within the overall range observed in gorillas and other non-human apes. Yet, more comparative data is needed to enhance our understanding of MTU geometry variety in non-human apes.

The comparative dataset further highlights the striking difference in teres major and pectoralis major position index between humans and the African apes (Table S 2). While all African ape indices lie above 20, and in the adults above 30, the human model indices are smaller than 20 for both muscles. However, more comparative data is needed to confirm an interspecific difference that is possibly indicating a functional signal.

MTU properties

Fiber length (L), pennation angle, maximum isometric force and tendon slack length determine the force potential of a MTU and are the basis of active and passive force calculation in OpenSim. Following van Beesel *et al.* (2021), maximum isometric force capacity (F_{max}) is calculated as:

$$F_{max} = 3.0 \times 10^5 \text{m}^{-2} m_{musc} (Ld)^{-1} \quad (1)$$

The muscle density (d) value ($1.06 \times 10^3 \text{ kg/m}^3$) and specific muscle tension ($3.0 \times 10^5 \text{ m}^{-2}$) have been used in other studies investigating mammals, including hominoids (Mendez, 1960; Ward and Lieber, 2005; O'Neill *et al.*, 2013; Goh *et al.*, 2017). Pennation angle is excluded from this equation, as it is accounted for in the muscle geometric calculations intrinsic to OpenSim (Bishop *et al.*, 2021). In order to virtually reconstruct the muscles that we added to the gorilla model, fiber length (L) and muscle mass (m_{musc}) of each MTU were collected during the dissection. After the muscles were taken off and tendons were removed, muscle mass was measured using an electronic balance ($\pm 0.01 \text{ g}$). Each measurement was repeated three times. Fiber length was determined through a maceration method (Reitsma, 1969; Alway *et al.*, 1989; Heron and Richmond, 1993) for all muscles except the subscapularis muscle. To macerate the muscles, the muscle belly is digested in 20% nitric acid solution for 24-48h, which afterwards allows for a cautious separation of the muscle fascicles. The muscle fascicles were transferred into petri dishes coated with glycerin, which terminates the digestion process, and digital photographs were taken. The photographs were used to measure the lengths of 10 to 20 fascicles per muscle in Fiji software (Schindelin *et al.*, 2012) and the average length was calculated. The average value was corrected for a 43% shrinkage that is introduced through the maceration method (Alway *et al.*, 1989; Heron and Richmond, 1993; van Beesel *et al.*, 2021). The corrected length was assumed to be equivalent to optimal fiber length (Zajac, 1989).

During the gorilla dissection, pennation angle was judged to be low for most muscles, except subscapularis. As the influence of pennation angles below 20° is negligible for muscle force calculation (Zajac, 1989; Thorpe *et al.*, 1999; Carlson, 2006), a representative value of 0° was used in the model. However, subscapularis displayed a noticeable pennation during dissection. Therefore, a different method was applied that allowed the simultaneous measurement of both muscle fiber length and pennation angle. Following the procedure described by Dickinson *et al.* (2018), the muscle belly was cut into different portions, following the orientation of muscle fascicles visible on the surface. The length of seven fascicles was measured using a digital caliper ($\pm 0.01 \text{ mm}$), as well as the perpendicular

distance between the fascicle's end point and the myotendinous sheet. Both lengths were used to calculate pennation angles.

Tendon slack length was estimated last. The estimation followed the equations developed by Manal and Buchanan (2004) and the approach detailed in Heers *et al.* (2018). The approach is based on the maximum feasible MTU length range over all degrees of freedom of each joint a muscle spans, which is estimated using the muscle analysis plotting tool of OpenSim. The MTU length range is especially influenced by joint and muscle geometry, including muscle wrapping.

The muscle architectural properties used in both models are presented in Table 3. The properties used in the human model are based on the values originally reported by Klein Breteler *et al.* (1999), calculated using the equation (1) and distributed to the same MTUs used in Seth *et al.* (2019).

Evaluation of MTU properties

Muscle soft-tissue properties estimated for our gorilla musculoskeletal model and previously published for other non-human apes are given in Table S 3. Additionally, F_{\max} values were normalized by body mass^{2/3} to improve the comparison (Davies and Dalsky, 1997; Folland *et al.*, 2008). Overall, the soft-tissue properties used in our gorilla model fall within the range observed in other non-human apes. Muscle mass, fiber length and F_{\max} values are smaller in our female than in the male gorillas, even when these were scaled to the same body mass. Muscle mass and fiber length of our female gorilla were either higher or similar than the values reported for chimpanzees, which resulted in higher (teres major and subscapularis) or similar (teres minor) F_{\max} values. However, normalized F_{\max} values were usually the smallest in our gorilla, except for subscapularis. The values estimated for our model showed the greatest overlap with the properties reported for the oldest (48 years) and the youngest (6 years) chimpanzee.

Therefore, the F_{\max} capacity relative to body mass of our female gorilla specimen appears to be at the lower end of the range observed in non-human apes. There are two possible explanations to this finding. Firstly, age-related muscle wasting occurred in our gorilla specimen, which reduced the overall force generating capacity. This explanation is supported by the similarity to other old and young specimens, which have small muscle masses relative to body mass (Thorpe *et al.*, 1999; Carlson, 2006). Secondly, sexual dimorphisms in gorillas could lead to relatively smaller force generating capacities in females than in males. This explanation would relate to an important point made in previous studies—that female gorillas are not miniaturized versions of males (Zihlman, 1992; Zihlman and McFarland, 2000; van Beesel *et al.*, 2021). Because existing comparative data were gathered from male specimens, our observations from a female contribute to understanding variation in ape musculoskeletal biology. Additionally, interspecific differences or non-allometric scaling effects lead to relatively high force generating capacities in chimpanzees compared to gorillas, which would result in female gorillas displaying the overall smallest force generating capacities within African apes. However, comparative muscle property data is limited in non-human apes. More comparative data is needed to investigate and verify intra- and interspecific differences.

Supporting Information 2 – Active fiber force-generating capacities

In OpenSim, MTU moment generating capacity is based on MA as well as active and passive force generating capacities. Active fiber force determines the moment ratio that can be generated through fiber activation and contraction. In our analyses, moment and active fiber force were estimated assuming maximal activation ($a=1$). In our gorilla model, we found that teres major and pectoralis major show the greatest muscle-tendon-length range. The force generating capacity of both MTUs changes substantially with arm position, compared to the results of the human model (Figure S2). Generally, the MTU force generating capacities of the gorilla model display similar trajectories as the corresponding MA curves, meaning that muscle forces peak at glenohumeral elevation angles where arm-lowering MAs are highest (Figure 3 (a) and Figure 4 (a)). This similarity indicates that episodes of enhancement in *Gorilla* compared to *Homo* are based on improved muscle force generating properties and skeletal morphology.

Teres major maximum force-generating capacity is predicted for the small glenohumeral elevation angles between 50° and 75° , and diminishes the more the arm is elevated. Between 40° and 85° , force capacity prediction is higher in the gorilla than in the human model. Therefore, greater *Gorilla* teres major active fiber force capacity and MA enhance the moment-generating capacity across smaller elevation angles as they might be used during quadrupedal walking, compared to *Homo* (Figure S2 and Figure 3).

In pectoralis major, force-generating capacity varies with glenohumeral elevation and elevation plane. Similarly as MA predictions (Figure 4 (a)), adduction (plane 0°) force capacity is high for small arm elevation angles, whereas retraction (plane 90°) force capacity is high when the arm is elevated. *Gorilla* force capacity is greater compared to *Homo* in the elevation planes 60° and 90° . In the elevation planes 0° and 30° , *Gorilla* force-generating capacity is greater compared to *Homo* at glenohumeral elevation angles below 40° and 70° , respectively. The greater *Gorilla* pectoralis major active fiber force capacity and MA enhance the moment-generating capacity across similar elevation angles. Due to the maxima occurring at different elevation angles in the different planes, the *Gorilla* pectoralis major enhancement covers a wide glenohumeral elevation range compared to *Homo* (Figure S2 and Figure 4).

Supplementary Information 3 – Sensitivity analysis

The development of musculoskeletal models necessitates making decisions about how specific musculoskeletal parameters are virtually represented. The nature of these decisions can have an effect on the results of the biomechanical analysis. While we took great care to develop our model in a similar way as the human model (Seth *et al.*, 2019), our aim was also to represent the morphology of our model specimen as closely as possible. We achieved this by dividing muscles into smaller subunits when anatomical separations were visible during the dissection. However, this caused a difference in the number of MTSUs of subscapularis and pectoralis major between the gorilla and human models. The number of subdivisions affects the position of attachment points and the orientation of muscle paths and MA predictions. We use a sensitivity approach to assess how these different decisions made during the model building process affect the performance results. By this, we evaluate whether differences or similarities observed between the model MA predictions result from actual interspecific differences or from modeling differences.

Pectoralis major sensitivity analysis

Based on observations during the dissection, we divided the pectoralis major into two MTSUs in the gorilla model, while the muscle is represented by three MTSUs in the human model (Figure S 3(a)). The muscle has a broad origin site in both species. The difference in number of MTSUs affects the way MTSUs origin points were distributed across this area. In order to evaluate whether a different, human-model-like, MTU separation affects the MA predictions, we developed three new representations of pectoralis major in the gorilla model and placed the origin positions similar to those used in the human model, but still remaining within the attachment areas observed in our gorilla specimen (Figure S 3(b)). The sensitivity of MA to the difference in MTSUs numbers and distributions is presented in an elevation plane of 0° (ab-/adduction) and 90° (pro-/retraction).

The results of the sensitivity analysis show that the arm-lowering mechanism is enhanced in *Gorilla* compared to *Homo*, regardless of MTSUs divisions and distributions. In the sternocostal pectoralis major, this is evident as all gorilla MTSUs (Thorax_M, Thorax_I and PecMajSternocost) show greater, more negative, MAs than their human model counterparts (Figure S 3(b)). In the plane of 90°, all gorilla clavicular pectoralis major MTSUs (PecMajClav and Clavicle_S) predict an arm-lowering action only, whereas the corresponding MTSU in the human model predicts a change from arm-raising to arm-lowering for glenohumeral elevation angles above horizontal. Therefore, although arm-lowering MAs of pectoralis major are sensitive to MTU division and origin position, the general conclusion that *Gorilla*-specific morphology enhances arm-lowering by higher MAs is still valid regardless of the different modeling decisions.

Subscapularis sensitivity analysis

The subscapularis muscle is represented as a single MTU in our gorilla model, but divided into three MTSUs in the human model. Similar to pectoralis major, this muscle has a wide origin area, which is covered to a greater extent by the three MTSUs used in the human model. We created two additional subscapularis MTSUs, one with a more superior and one with a more inferior origin position, to evaluate how MTU division and distribution affect arm-lowering MA prediction (Figure S 4). MA sensitivity is evaluated in an elevation plane of 0° (ab-/adduction) and 90° (pro-/retraction).

The results of the analysis support the finding that arm-lowering performance is similar between *Gorilla* and *Homo* (Figure S 4). The predicted MAs of the gorilla model are less sensitive to MTU division and distribution than in the human model. In the gorilla model, the original MTU is located between the superior and inferior subunits in the sensitivity analysis. In an elevation plane of 0°, the resulting MA curve approximates the average of the more superior and more inferior MTSUs. In an

elevation plane of 90°, the original gorilla subscapularis MA curve is closer to the estimated MA of the inferior than the superior subunit, similar as in the human model.

Tables

Table S 1. The muscle wrapping surfaces of the gorilla model restrict the muscle path and prevent muscle-bone intersection. Locations, shapes and dimensions of wrapping surfaces similar to those used in Seth *et al.* (2019) were selected. A dagger (†) indicates deviations necessary to account for gorilla-specific anatomy.

Muscle(s)	Location	Shape	Dimensions (in m)		
			A	B	C
Teres Major	Thorax, Ribcage	Ellipsoid	0.094†	0.181†	0.083†
Teres Minor	Scapula† subscapular fossa	Ellipsoid	0.046	0.101	0.050
Subscapularis	Scapula, Glenoid surface	Ellipsoid	0.0350	0.097	0.015
Subscapularis	Humerus, Head	Ellipsoid	0.030	0.034	0.030
Pectoralis Major	Thorax Ribcage	Ellipsoid	0.111	0.208	0.102
Teres Minor	Humerus head	Sphere	0.031†	0.031†	0.031†

Table S 2. Position index of glenohumeral arm-lowering muscles. The distance of muscle insertion to top was measured for muscles of gorilla and human models and used to calculate the position indices. Indices reported in other studies are presented additionally.

		Teres Major	Teres Minor	Pectoralis major	Subscapularis
Gorilla model	Distance to Top (m)	0.127	0.029	0.114	0.035
	Position Index	35.376	8.078	31.616	9.749
Human model	Distance to Top (m)	0.062	0.032	0.060	0.023
	Position Index	19.018	9.816	18.252	7.055
Gorilla (Stewart, 1936)	Position Index			28.2	
Chimpanzee (Stewart, 1936)	Position Index			24.3	
Chimpanzee (Fleagle and Simons, 1982)	Position Index	34			

Table S 3. Comparative MTU properties reported in this study and in the literature. F_{max} was calculated using equation (1). In cases where previous studies reported observations on multiple specimens, we list only the most comparable specimen (based on body mass, age and sex) or the most complete data. m, muscle mass; L, muscle fiber length; F_{max} , maximum isometric force; Norm F_{max} , F_{max} normalized by body mass^(2/3).

Muscle	Parameter	This study	Kikuchi and Kuraoka (2014)	Payne (2001)	Carlson (2006)	Kikuchi et al. (2012)	Oishi et al. (2009)	Thorpe et al. (1999)
	Species	<i>Gorilla gorilla</i>	<i>Gorilla gorilla</i>	<i>Gorilla gorilla</i>	<i>Pan troglodytes</i>	<i>Pan troglodytes</i>	<i>Pan troglodytes</i>	<i>Pan troglodytes</i>
	Body mass (kg)	80	-	120 scaled to 80	54.7	32.2	30.2	37
	Sex	Female	Male	Male	Female	Female	Female	Male
	Age	49	-	30	48	Adult	11	6
Teres major	m (kg)	0.103	0.240	0.221	0.115		0.099	0.073
	L (m)	0.119	0.165	0.170	0.130		0.127	0.142
	F_{max} (N)	244.329	409.984	368.608	251.234		219.507	145.496
	Norm F_{max}	2.872		4.333	3.805		4.940	2.860
Teres minor	m (kg)	0.025	0.040	0.059	0.014		0.021	0.021
	L (m)	0.080	0.089	0.109	0.046		0.062	0.068
	F_{max} (N)	89.504	125.328	153.780	86.136		93.579	87.403
	Norm F_{max}	1.052		1.808	1.305		2.106	1.718
Subscapularis	m (kg)	0.239	0.374		0.095	0.110	0.155	
	L (m)	0.062	0.095		0.063	0.028	0.058	
	F_{max} (N)	1087.185	1110.990		425.427	1126.436	755.856	
	Norm F_{max}	12.781			6.444	24.292	17.012	
Pectoralis major clavicularis	m (kg)	0.079		0.135				
	L (m)	0.120		0.144				
	F_{max} (N)	187.605		265.121				
	Norm F_{max}	2.205		3.117				
Pectoralis major sternocostalis	m (kg)	0.108		0.247	-			
	L (m)	0.109		0.181	0.208			
	F_{max} (N)	280.069		444.887	-			
	Norm F_{max}	3.292		5.230				

Figures

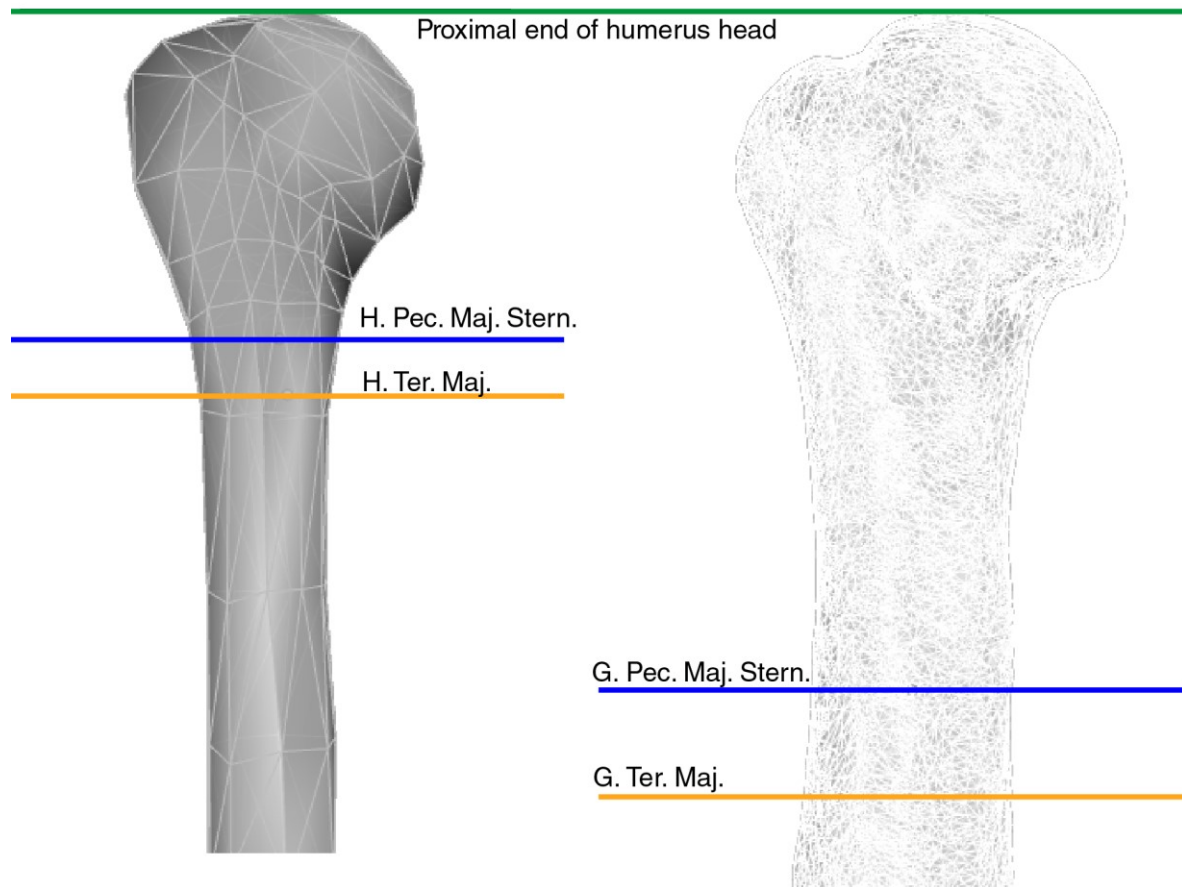


Figure S 1. Humeral attachment positions relative to proximal end of humerus head. Positions of teres major (Ter. Maj., orange) and pectoralis major sternocostalis (Pec. Maj. Stern., blue) are highlighted on the gorilla humerus (G., right, in white) and on the human humerus (H., left, in grey).

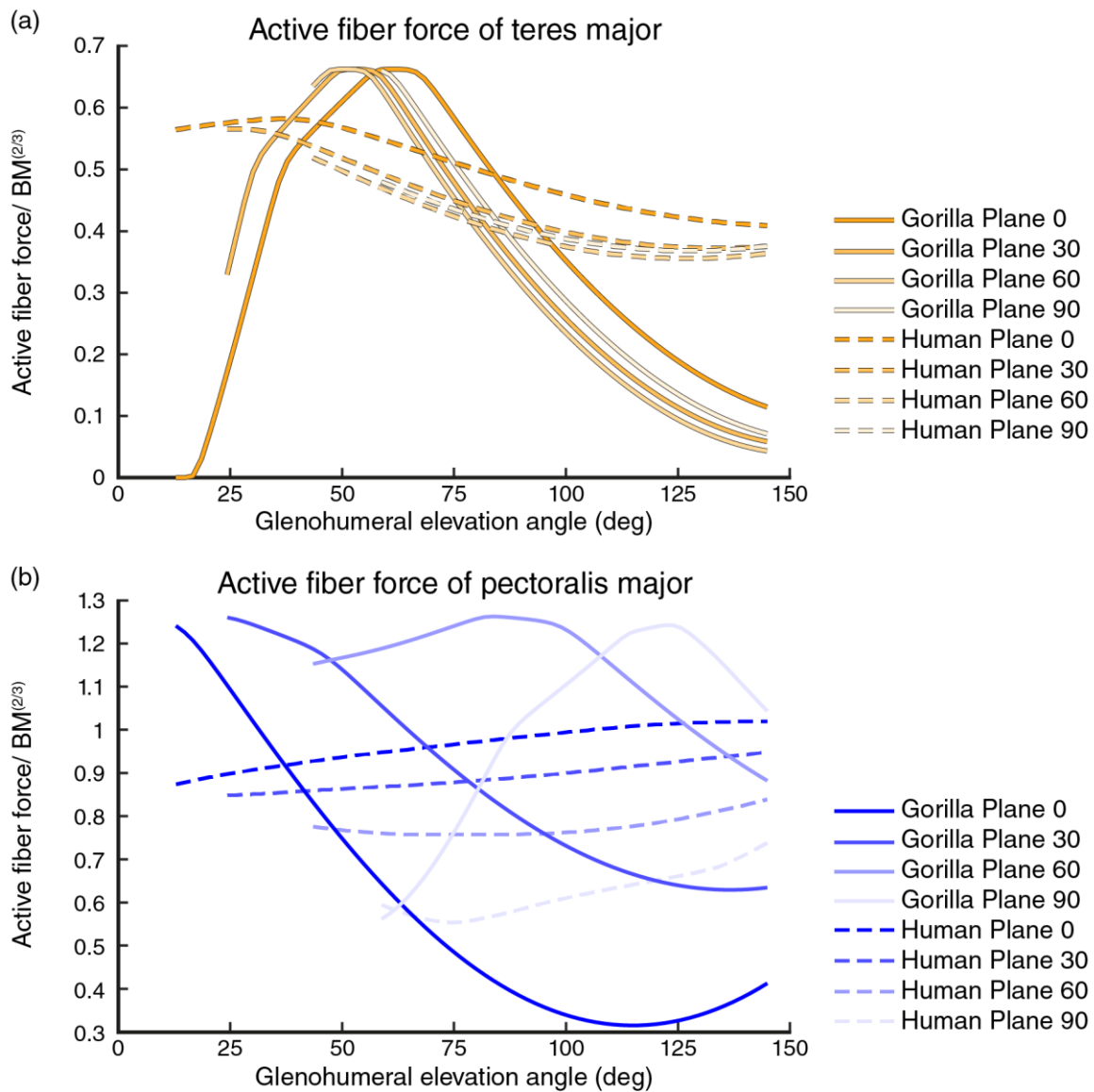


Figure S 2. Active fiber force generating capacity of teres major (a) and pectoralis major (b) in the gorilla (solid) and human (dashed) musculoskeletal models. The grey bar highlights the range of glenohumeral elevation angles utilized during vertical climbing. The grey striped bar highlights the range of joint angles exploited during quadrupedal walking.

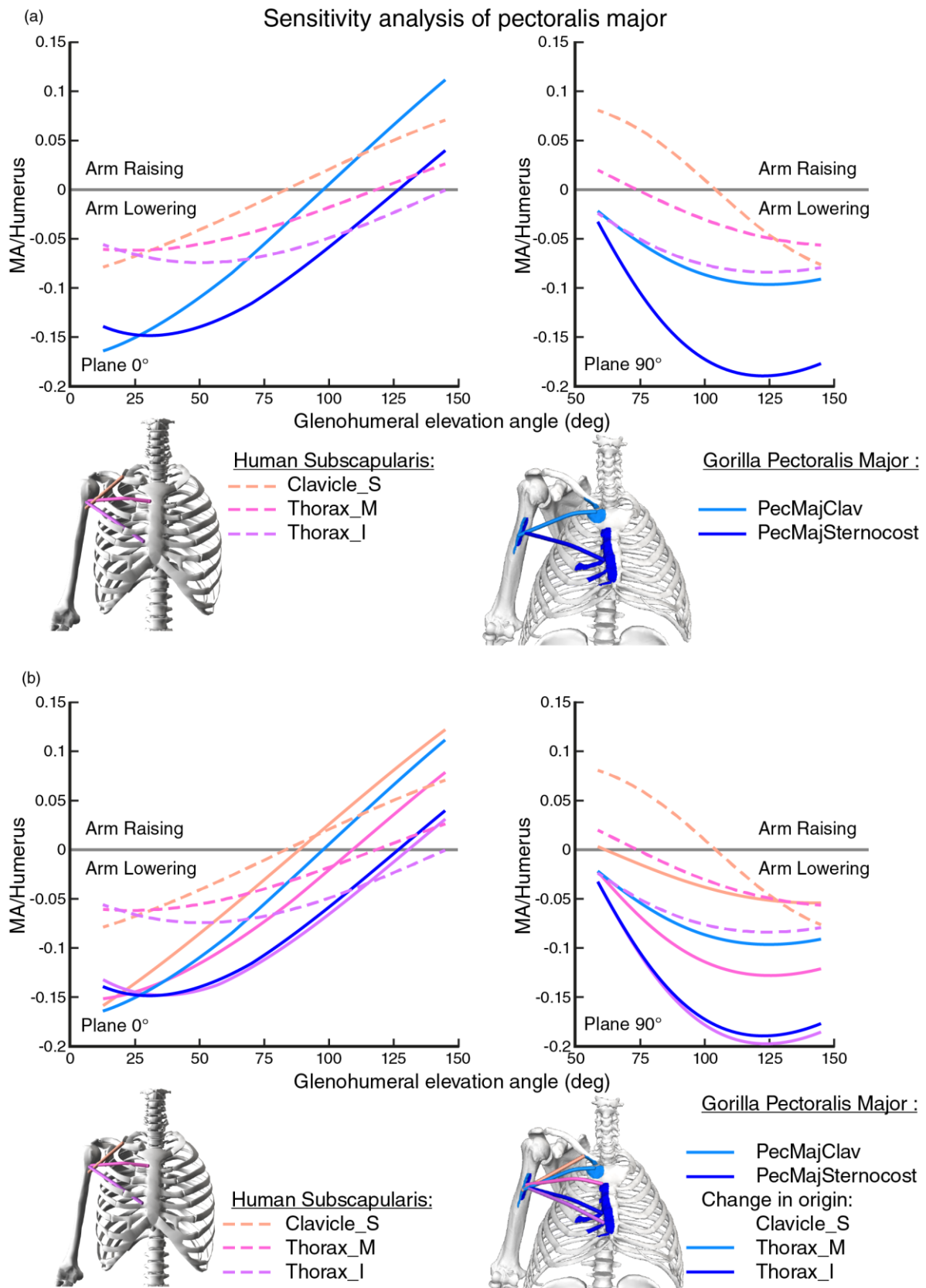


Figure S 3. Sensitivity analysis of pectoralis major. The model pictures show the distribution of the MTSUs. The colored areas on the gorilla model highlight the attachment areas of clavicularis and sternocostalis pectoralis major. (a) MA of the pectoralis major MTSUs of the human and gorilla models. (b) MA of pectoralis major MTSUs of both models together with MAs predicted for the three new gorilla MTSUs with different origin positions.

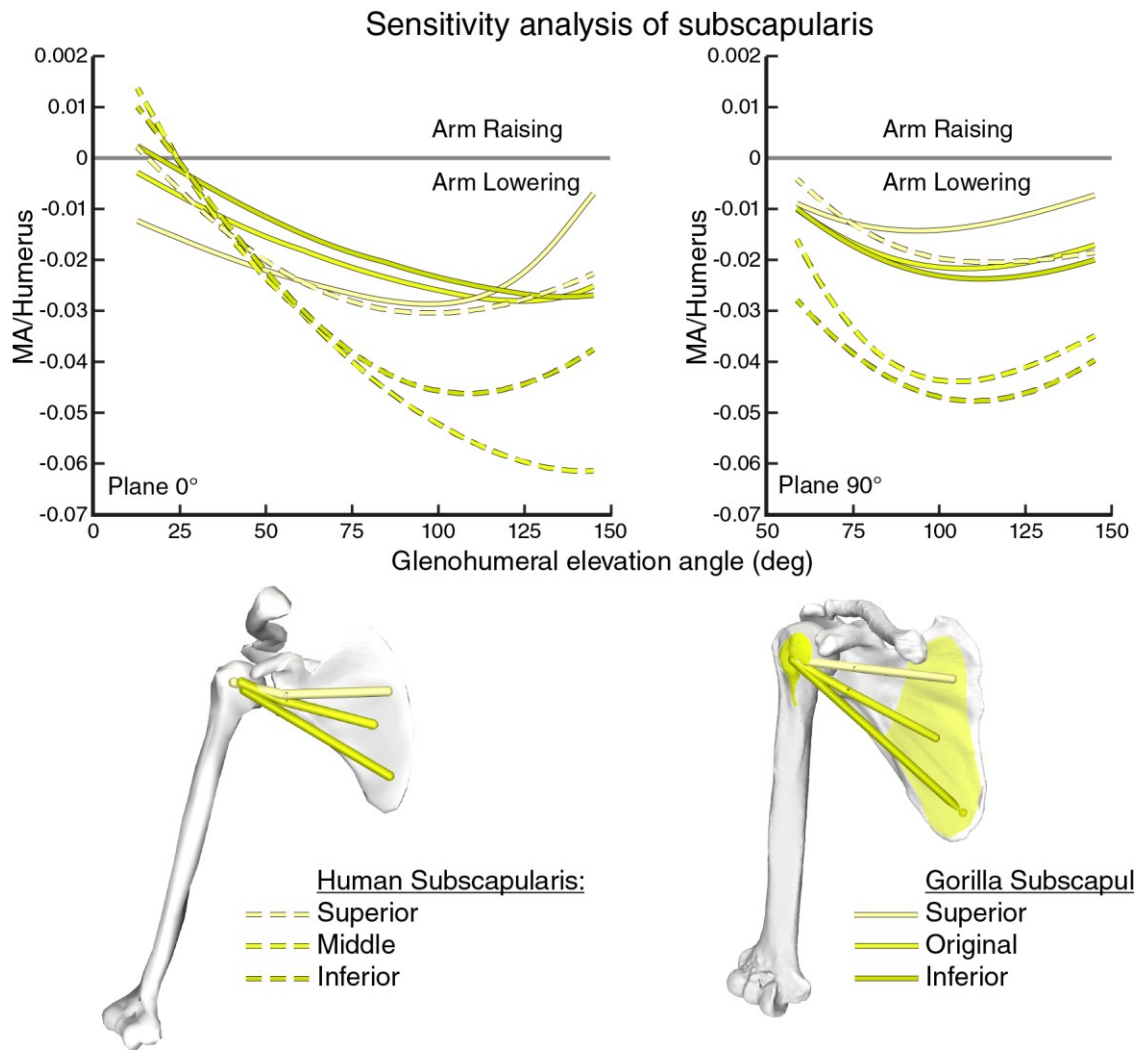


Figure S 4. Sensitivity analysis of subscapularis. The model pictures (bottom) show the distribution of the MTSUs. The colored areas on the gorilla model highlight the attachment areas of subscapularis. The MA of subscapularis as it is originally represented in the gorilla model, together with two new MTSUs (one with superior, one with inferior origin) is presented together with MAs predictions of the three human model MTSUs.

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Appendix C

Curriculum Vitae

Curriculum Vitae

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EDUCATION

- 2017 - present Ph.D. candidate, Max Planck Institute for Evolutionary Anthropology and Leipzig University
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 Supervisors: Prof. Jean-Jacques Hublin, Dr. Stephanie Melillo
- 2016 M.Sc. Evolution, Ecology and Systematics, Friedrich-Schiller-University Jena
 Dissertation title: Grooming movements of the rat (*Rattus norvegicus*, Muridae, Rodentia) – a kinematic analysis
 Supervisor: PD Dr. Manuela Schmidt, Prof. Martin Fischer
- 2013 B.Sc. Biology, Friedrich-Schiller-University Jena

ACADEMIC APPOINTMENTS AND RESEARCH EXPERIENCE

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| 2017-present | Max Planck Institute for Evolutionary Anthropology | <u>Doctoral Researcher</u> , Biomechanical analysis of the hominoid shoulder, performance comparison between <i>Gorilla</i> and <i>Homo</i> using musculoskeletal models, developed using Matlab, SIMM and OpenSim |
| 2014-2017 | Friedrich-Schiller-University Jena | <u>Research Assistant</u> , Grooming movement of rats and locomotion of rats and dogs, data analysis via SIMI Motion®, 3-D kinematic analysis via XROMM (Autodesk Maya) |
| 2011-2016 | Max Planck Institute for Chemical Ecology Jena | <u>Research Assistant</u> , Odor perception of <i>Drosophila melanogaster</i> , 3D reconstructions of neurons via Amira®, Immuno-staining, Imaging |

PEER-REVIEWED PUBLICATIONS

- 2022 **van Beesel J**, Hutchinson JR, Hublin J-J, Melillo SM. Comparison of the arm-lowering performance between *Gorilla* and *Homo*. *American Journal of Biological Anthropology*.
- 2022 Demuth OE, Wiseman ALA, **van Beesel J**, Mallison H, Hutchinson JR. Three-dimensional polygonal muscle modelling and line of action estimation in living and extinct taxa. *Scientific reports* doi:10.1038/s41598-022-07074-x
- 2021 **van Beesel J**, Hutchinson JR, Hublin J-J, Melillo SM. Exploring the functional morphology of the *Gorilla* shoulder through musculoskeletal modelling. *Journal of Anatomy*. doi:10.1111/joa.13412

CONFERENCE ABSTRACTS

- 2021 **van Beesel J**, Hutchinson JR, Hublin J-J, Melillo SM. Comparison of the arm-lowering performance between *Gorilla* and *Homo*. Presented at the 11th Annual meeting of the European Society for the study of Human Evolution
- 2021 **van Beesel J**, Hutchinson JR, Hublin J-J, Melillo SM. Comparison of shoulder functional morphology between *Gorilla* and *Homo*. Presented at the 90th Annual Meeting of the American Association of Physical Anthropologists
- 2020 **van Beesel J**, Hutchinson JR, Hublin J-J, Melillo SM. Modelling musculoskeletal systems to investigate arm-raising adaptations in hominoids. Presented at the Young Researcher Morphology Meeting in Vienna
- 2019 **van Beesel J**, Goldner F, Myatt J, Hublin J-J, Melillo SM. Fiber-type distribution in the shoulder muscles of hominoids: implications for a link between muscle architectural parameters and locomotor modes. Presented at the 112th Annual Meeting of the German Zoological Society (DZG) in Jena

Place, Date

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Appendix D

Author Contributions



March 14, 2022

Declaration of Independence

I hereby declare that I have conceived and written the thesis "*Biomechanical consequences of variation in shoulder morphology in the Hominoidea*" independently, without any inadmissible help and without using resources other than those stated. All direct and indirect quotations from the work of others have been clearly identified as such. I have not previously attempted to complete this or any other doctorate degree.

Julia van Beesel

Author contribution statement

Julia van Beesel

Biomechanical consequences of variation in shoulder morphology in the Hominoidea

Author contribution statement

Title: Exploring the functional morphology of the *Gorilla* shoulder through musculoskeletal modelling

Journal: Journal of Anatomy (Published)

Authors: Julia van Beesel, John R. Hutchinson, Jean-Jacques Hublin, Stephanie Melillo

Julia van Beesel (First author):

- Project idea
- Study design
- Data collection
- Data analysis
- Writing of the manuscript

Jean-Jacques Hublin (Author 3):

- Funding acquisition

Stephanie M. Melillo (Senior author):

- Project idea
- Study design
- Data collection
- Comments on the manuscript

John R. Hutchinson (Author 2):

- Comments on the study design
- Supporting Data analysis
- Comments on the manuscript



 Julia van Beesel



 Stephanie Melillo

Author contribution statement

Julia van Beesel**Biomechanical consequences of variation in shoulder morphology in the Hominoidea**

Author contribution statement

Title: Comparison of the arm lowering performance between *Gorilla* and *Homo* through musculoskeletal modelling.

Journal: American Journal of Physical Anthropology (Published)

Authors: Julia van Beesel, John R. Hutchinson, Jean-Jacques Hublin, Stephanie Melillo

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