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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

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

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(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

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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 addictions 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
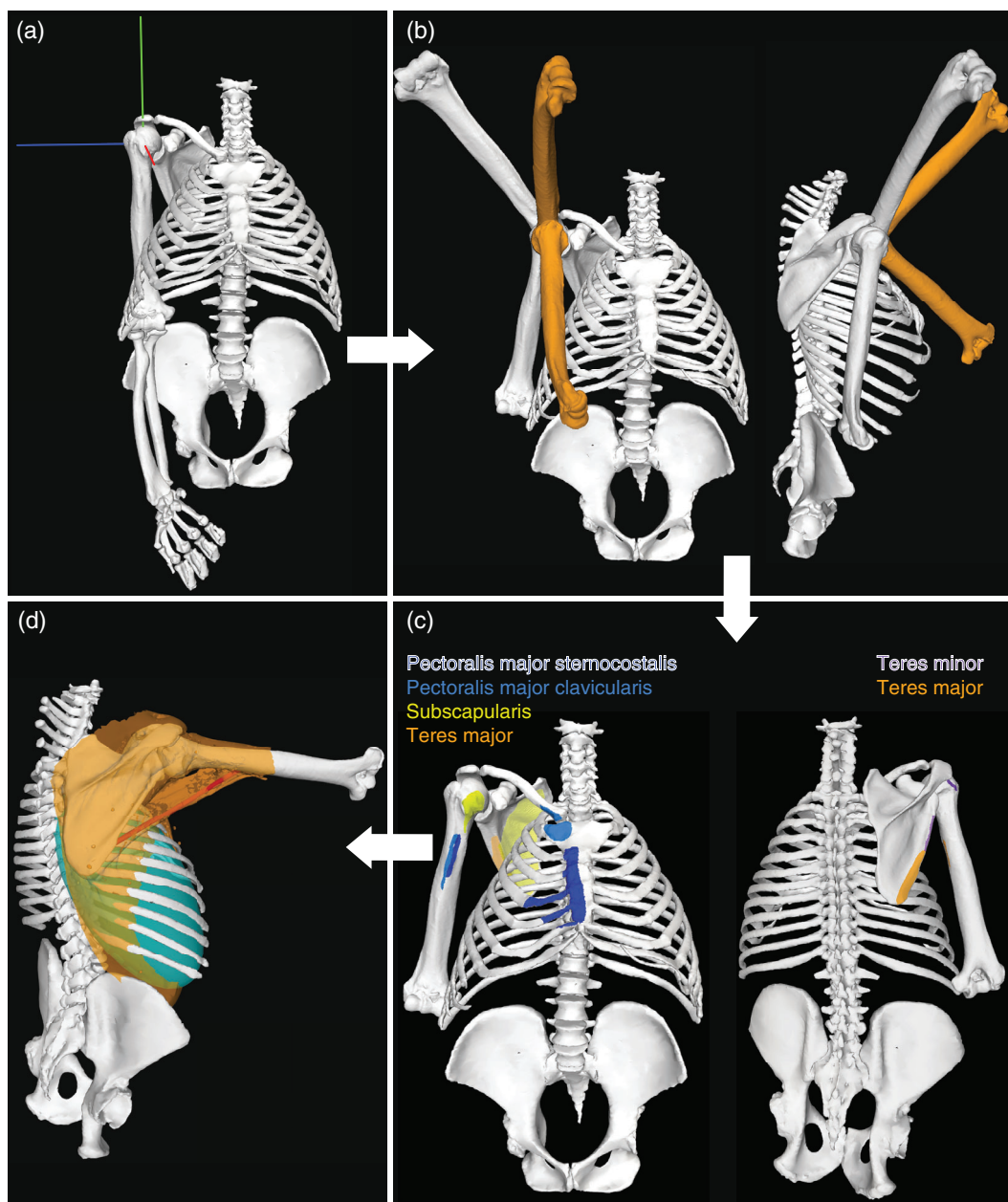
FIGURE 1 Workflow of model editing. (a) View from the front, model is in zero position (all joint angles set to zero). Axes of the humeral anatomical coordinate system are displayed, x-axis in red, y-axis in green, z-axis in blue. (b) Minimum and maximum shoulder elevation in the elevation planes of 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

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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^t_s(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^t_s, 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°)
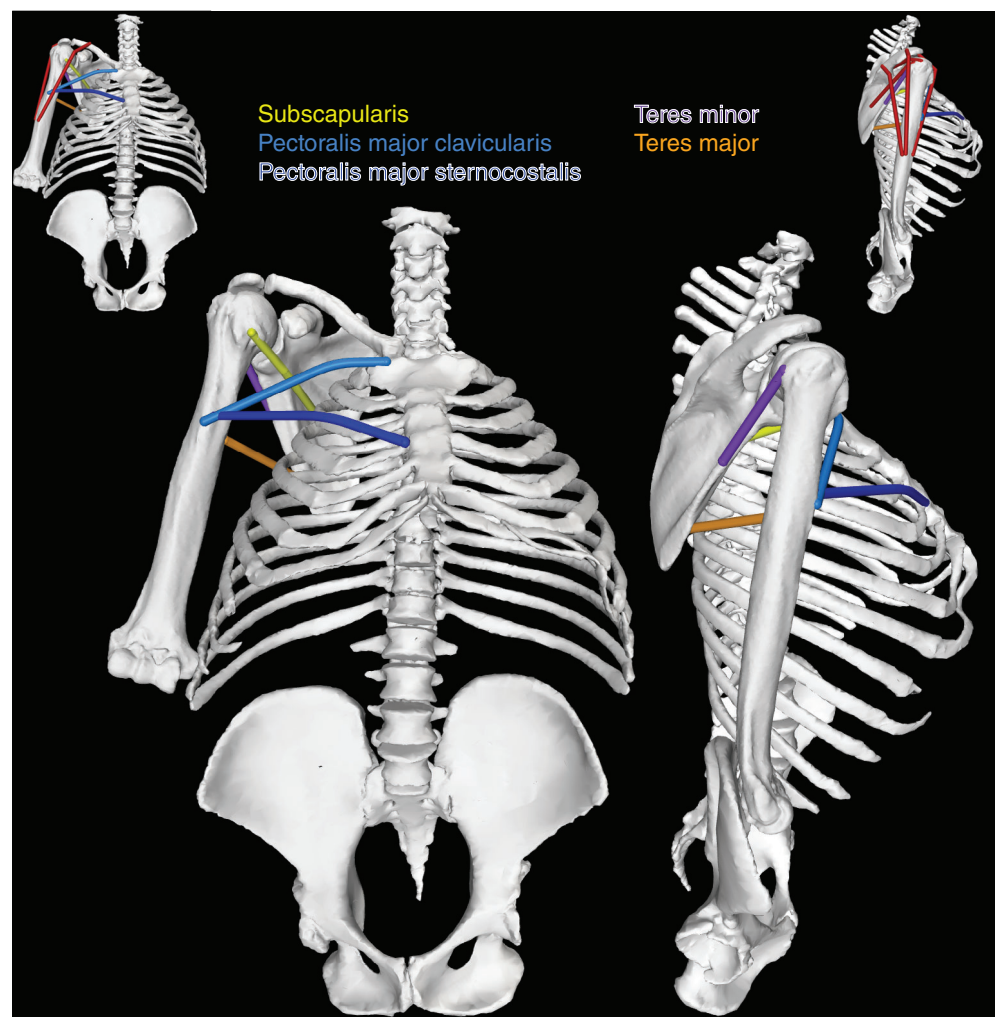
affected by the plane in which the arm is raised. In both species, the largest negative MA values are predicted when the arm is in a lowered position and the curves course upward the higher the arm is elevated. However, there is a marked difference in the magnitude of teres major MAs between models. 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.
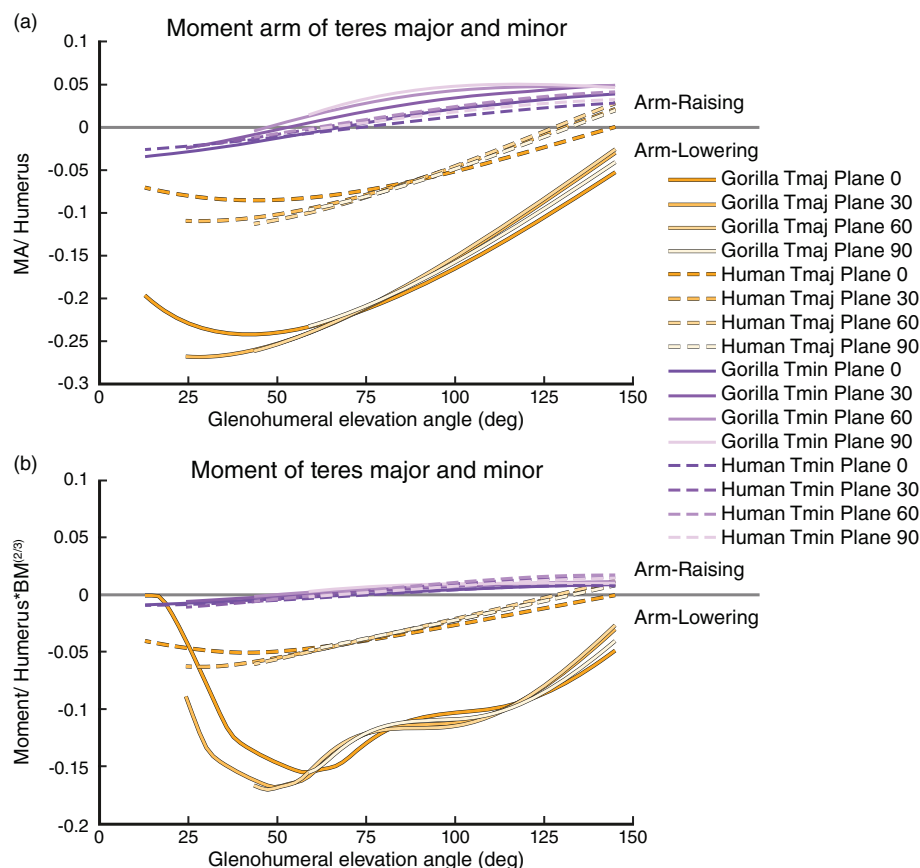
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FIGURE 3 MA normalized by humerus length and moment normalized by humerus length times body mass$^{(2/3)}$ of teres major (Tmaj) and minor (Tmin) muscle. Positive values predict an arm-raising, negative values an arm-lowering action of the MTUs

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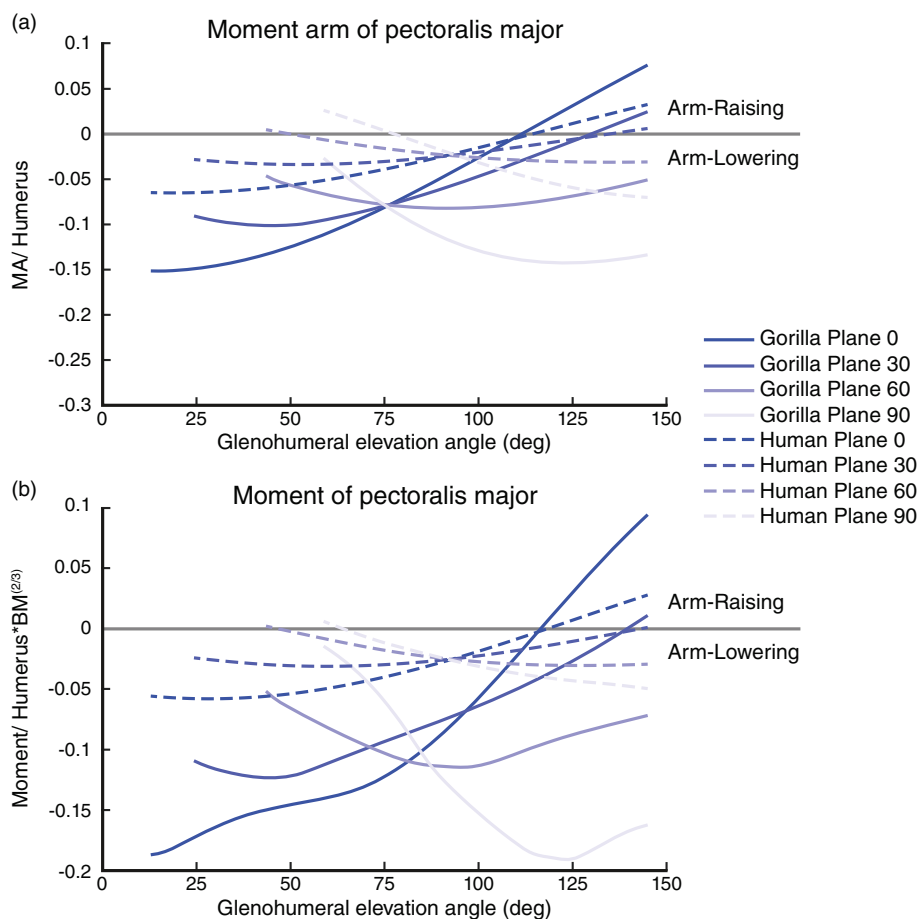
arm-lowering action is predicted for both models and in all planes. Overall, MA remains relatively constant over the course of arm elevation (Figure 5a).

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.
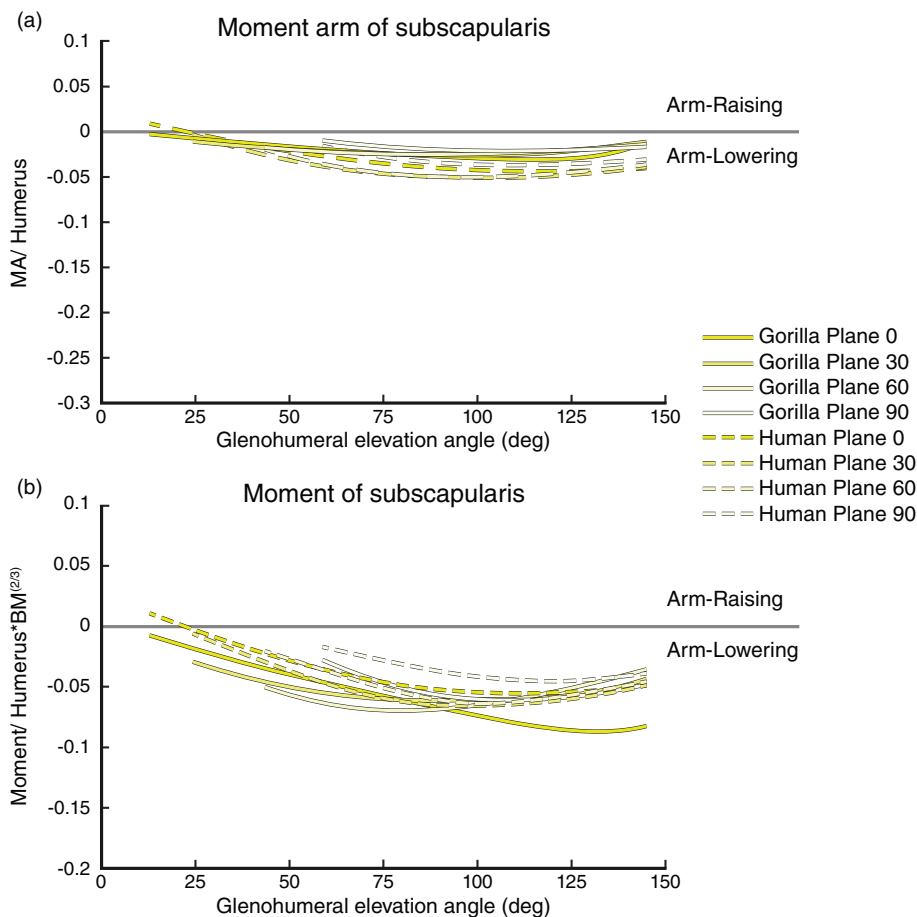
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(a)

Moment arm of subscapularis

(b)

Moment of subscapularis

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)
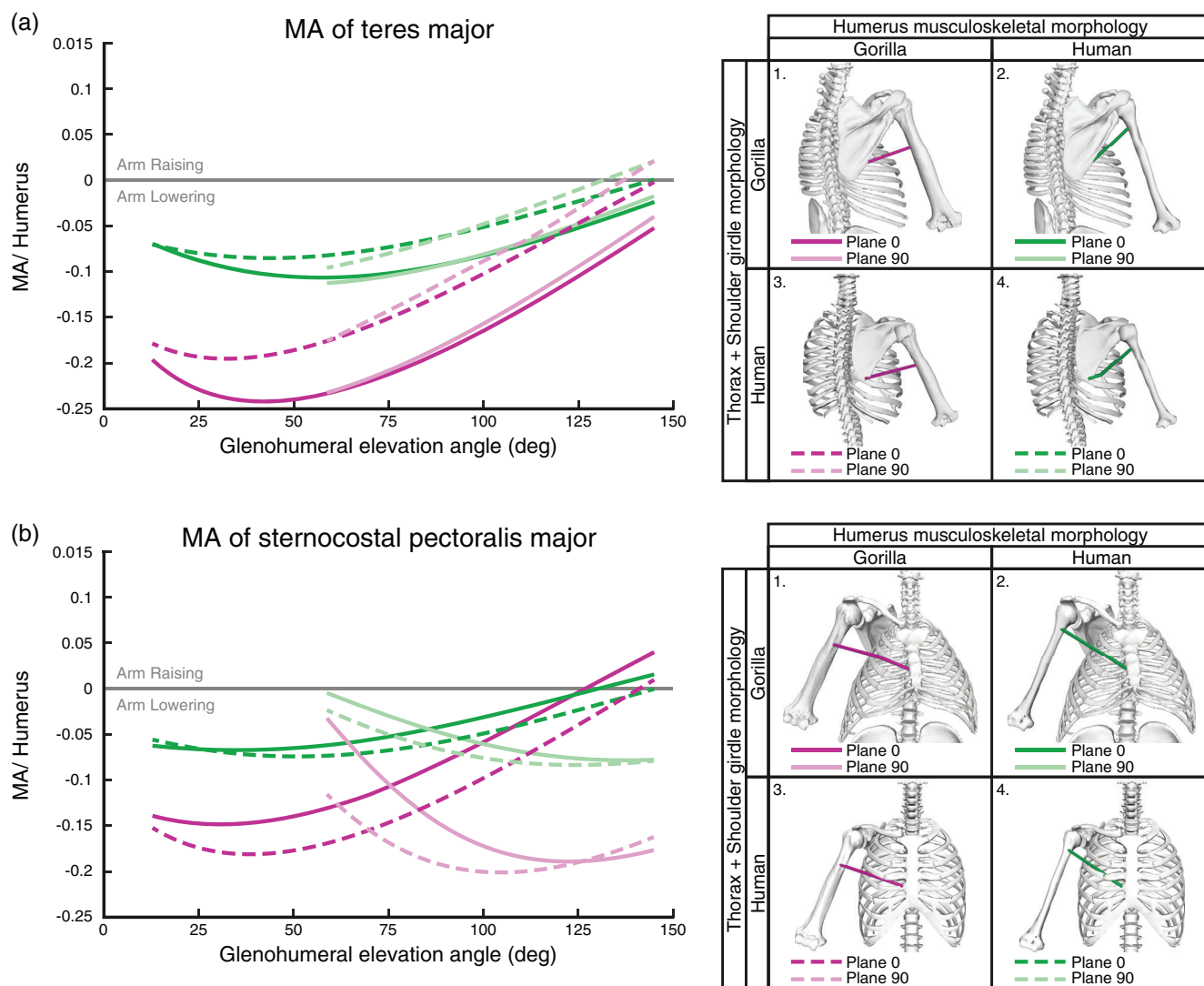
FIGURE 6 Biomechanical consequence of shoulder morphological variation for teres major (a) and sternocostal pectoralis major (b). The line style separates the gorilla (solid) from the human (dashed) thorax and shoulder girdle morphology, while the line color separates the gorilla (pink) from the human (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).
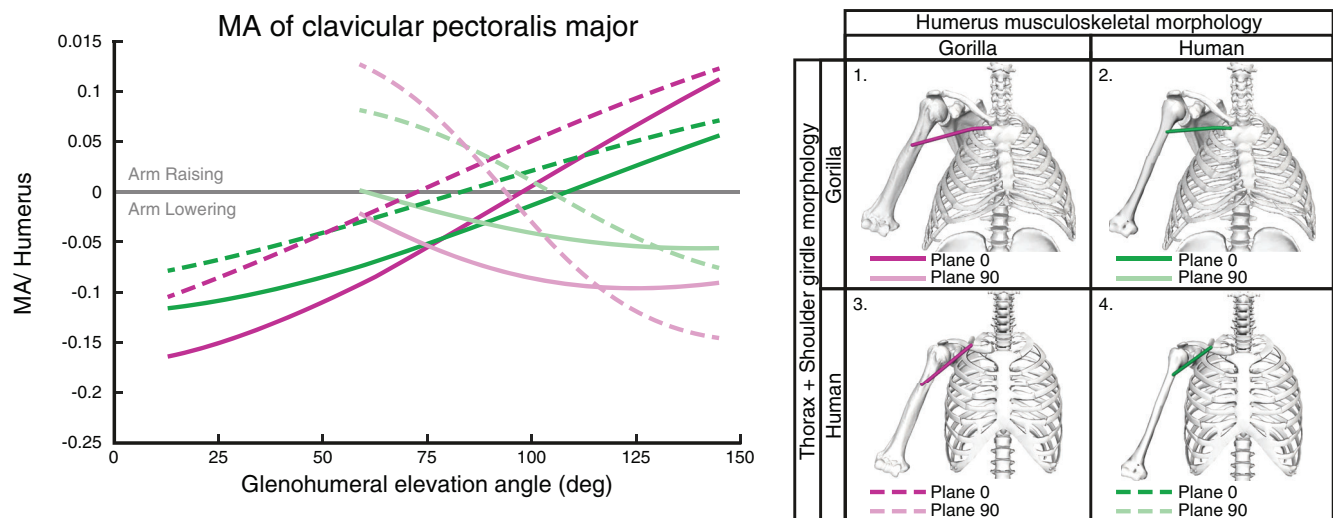
FIGURE 7 Biomechanical consequence of shoulder morphological variation for clavicular pectoralis major. The line style separates the gorilla (solid) from the human (dashed) thorax and shoulder girdle morphology, while the line color separates the gorilla (pink) from the human (green) humerus morphology. 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
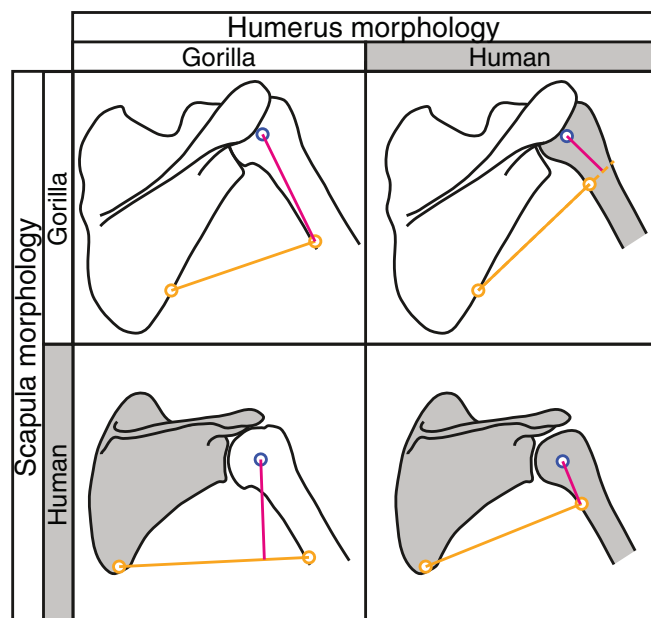
FIGURE 8 Effects of different musculoskeletal features on teres major MA. *Gorilla* skeletal morphology is in white, *homo* skeletal morphology in gray. GHJ center is highlighted using a blue circle. Teres major muscle path (orange) is the linear connection between muscle attachment points (orange circle). 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

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

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
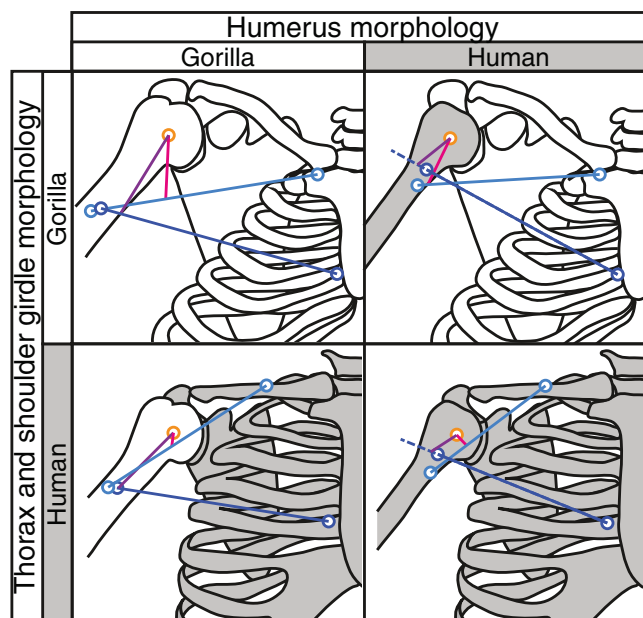
clavicular pectoralis major might somewhat trade-off the decreasing effect observed in sternocostal pectoralis major. Furthermore, the inferior muscle origin relative to GHJ position results in a more lateral fiber orientation of the clavicular portion of pectoralis major, in contrast to what is observed 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.

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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

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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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