Development of a Probabilistic Chimpanzee Glenohumeral Model: Implications for Human Function

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Modern human shoulder function is affected by the evolutionary adaptations that have occurred to ensure survival and prosperity of the species. Robust examination of behavioral shoulder performance and injury risk can be holistically improved through an interdisciplinary approach that integrates anthropology and biomechanics. Anthropological research methods have attempted to resolve gaps in human shoulder evolution, while biomechanics research has attempted to explain the musculoskeletal function of the modern human shoulder. Coordination of these two fields can allow different perspectives to contribute to a more complete interpretation of, not only how the modern human shoulder is susceptible to specific injuries, but also why.

How the modern human shoulder arose from a, likely, weight-bearing, arboreal past to its modern form, and what this has meant for modern behaviors, is not well understood. Despite a weight-bearing, locomotor ancestral usage, the modern human upper extremity is highly fatigable in repetitive, low to moderate force tasks, such as overhead reaching. The closest living human relative, modern chimpanzees, has retained an arboreal, locomotor upper extremity. Interdisciplinary comparative research on humans and chimpanzees could lead to greater insight on modern human shoulder function. The purpose of this research was to explore the modern human capacity for ancestral, brachiating behaviors and resultant injury mechanisms through comparative experimental, computational modeling and probabilistic modeling approaches with chimpanzees.

The first study experimentally explored the modern human ability to perform a horizontal bimanual arm-suspensory climbing task. EMG of 12 upper extremity muscles and motion capture of the arm and thorax were monitored in experienced and inexperienced climbers. Results were also compared to previously published or collected data on chimpanzees performing an analogous task. While all human climbers used a high proportion of their muscular reserve to perform the task, experienced climbers had moderately reduced muscle activity in most muscles, particularly during phasic shifts of the climb cycle and moderately more efficient kinematics. Climbing kinematics and muscle activity were very similar between humans and chimpanzees. However, chimpanzees appear to have a different utility of the posterior deltoid, suggesting an influence of their habitual arboreal behaviors.

The second and third studies describe the development of a deterministic chimpanzee musculoskeletal glenohumeral model. Study 2 developed geometric parameters of chimpanzee shoulder rhythm and glenoid stability ratios for the construction of a chimpanzee glenohumeral model. The chimpanzee glenohumeral model of Study 3 was designed to parallel an existing human glenohumeral model, enabling comparative analyses. The chimpanzee glenohumeral model consists of three modules – an external torque module, musculoskeletal geometric module, and an internal muscle force prediction module. Together, these modules use postural kinematics, subject specific anthropometrics and hand forces to estimate joint reaction forces and moments, subacromial space dimensions, and muscle and tissue forces. Using static postural data from Study 1, predicted muscle forces and subacromial space were compared between chimpanzees and humans during an overhead, weight-bearing climbing task. Compared to chimpanzees, the human model predicted a 2mm narrower subacromial space, deltoid muscle forces that were often double those of chimpanzees and a strong reliance on infraspinatus and teres minor (60-100% maximal force) over other rotator cuff muscles.

Finally, the deterministic chimpanzee and human glenohumeral models were expanded in Study 4 to a probabilistic analysis of rotator cuff function between species. Using probabilistic software and the same postural climbing inputs, both models had anthropologically relevant musculoskeletal features perturbed in a series of Monte Carlo simulations – muscle origins and insertions, glenoid inclination and glenoid stability – to determine if rotator cuff muscle force prediction distributions would converge between species. Human rotator cuff muscle behavior did not converge with chimpanzees using probabilistic simulation. The human model continued to predict strong dependence on infraspinatus and teres minor, with 99% confidence intervals of [0-100]% maximal force, over supraspinatus and subscapularis, with confidence intervals of [0-5]% maximal force. Chimpanzee rotator cuff confidence intervals were typically between [0-40]% maximal force, with median force for all four rotator cuff muscles typically 5-20% maximal force. While perturbation of muscle origins and insertions had the greatest effect on muscle force output distributions, no musculoskeletal variation notably modified human climbing performance.

Structural musculoskeletal differences between species dictated differences in glenohumeral function. The results from all studies indicate susceptibility for the fatigue-induced initiation of subacromial impingement syndrome and rotator cuff pathology in modern humans during overhead and repetitive tasks. Lower muscle absolute PCSA in humans, combined with a laterally oriented glenohumeral joint and laterally projecting acromion reduced the capacity for overhead postures and weight-bearing postures. These evolutionary differences may have been vestigial consequences, concurrent with necessary adaptions for important, evolutionary human-centric behaviors such as throwing. However, they have influenced the high rates of rotator cuff pathology in humans compared to closely related primates.

The present work represents an important first step toward a broad scope of future research. Interdisciplinary computational modeling offers an evolving and improving alternative to traditional methods to study human evolution and function. Computational and probabilistic simulations can be expanded to numerous other biomechanical and evolutionary queries. The results of this thesis are a promising initial step to examining the evolutionary structural connection to biomechanical human function through comparative computational modeling.

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Chapter 1 Introduction

Humans are fascinated by their history, from personal stories to the collective human ancestry. What defines humanity and where humans came from has driven much of the scientific interest in human evolution. When The Beagle set sail in 1831, Charles Darwin began to lay the foundation for the Theory of Evolution, seeking to explain observed species diversity through the idea that species adapt to their environments, and develop physical capabilities that are specialized to their way of life (Alexander, 2004; Green & Alemseged, 2012). The study of evolution has provided an ongoing means of placing humanity within its proper historical, genetic, geographical and morphological rank in the animal kingdom. Scientific pursuit, including the field of biomechanics, seeks to examine the diversification of the animal kingdom and where human evolution fits into the ongoing evolution of life. For the biomechanist, this question becomes centered on how and why different animals and humans locomote and move the way they do (Pronk, 1991).

1.1 Human Evolution and Modern Upper Extremity Capacity

Humans evolved from a primate lineage along with the great apes chimpanzees, bonobos, gorillas and orangutans (Oxnard, 1969). The closest living relative to humans is the chimpanzee, with whom humans share a vast amount of genetic DNA and morphological traits (Patterson, 2006). Humans and chimpanzees split to form their own lineage approximately 5.4 million years ago (Patterson, 2006). Based on fossilized remains, humans and chimpanzees appear to have evolved from a common arboreal, tree-climbing or quadrupedal terrestrial ancestor (Kivell & Schmitt, 2009; Niemitz et al., 2010). A series of evolutionary morphological adaptations have changed humans from creatures with a weight-bearing, locomotor upper extremity to the terrestrial bipedal creature of today (Lovejoy, 2005; Wood, 2010). Conversely, chimpanzees have retained arboreal and brachiating capacity, as well as terrestrial locomotor abilities (Larson, 1988). The evolutionary chain of events that brought about the modern human form is still debated.

Specialized behavioral features for species are often found in the upper and lower extremity, providing insight into an animal's physical and social behaviors (Green & Alemseged, 2012). Terrestrial bipedal posture has been considered a crucial marker of humanity, distinguishing humans from apes and other animals. But how and why the series of physical adaptations that led to the present human bipedal lower extremity and non-weight-bearing upper extremity occurred, and what came before is still highly debated. It has been hypothesized that the benefits of standing on two feet is demonstrated in the upper extremity, through the freeing of the hands for feeding, tool and weapon use, as well as carrying (Darwin, 1871). The human upper extremity is unique in its capacity for powerful overhead throwing (Churchill & Rhodes, 2009), as well as fine motor control that allows for a variety of tool use and manipulation (Walker, 2009). However, the human upper extremity is also vulnerable to injury and disorders in sustained and repetitive overhead postures (Cote & Bement, 2010; Marras et al., 2006). Both the unique capacity and limitations of the human upper extremity are rooted in the specialized musculoskeletal features evolved in the body region.

A propensity for injury in overhead postures seems contradictory to the evolutionary history of humans. Subacromial impingement syndrome, which often leads to rotator cuff pathology and tears, accounts for up to 65% of all human shoulder disorders (Neer, 1983; van der Windt et al., 1995). Repetitive, fatiguing, overhead work is often implicated in the development subacromial impingement, making such postures problematic in modern humans (Cote & Bement, 2010; Dickerson et al., 2011). This is surprising, as humans likely evolved from an ancestor that spent a great deal of time brachiating and climbing in overhead, weight-bearing postures (Larson, 2015; Lewis et al., 2001). The musculoskeletal features of the upper extremity that influence capacity for overhead postures are not fully understood (Lewis et al., 2001). Comparison with species that retain a greater overhead capacity than modern humans could inform the understanding of why the modern human upper extremity is so prone to overhead and fatigue-related injuries.

Specific musculoskeletal features that diverge between species could be indicative of those that influence the modern human risk for rotator cuff pathology.

Exploration of the chimpanzee upper extremity may provide answers to the perplexing scenario of human overhead capacity. Humans and chimpanzees have similar functional upper extremity abilities, with divergent primary functions. Though closely related, both genetically and morphologically, chimpanzees have retained arboreal overhead capacities (Larson, 1988). Of the viable comparative species, chimpanzees also represent one of the best documented, with a wide breadth of available musculoskeletal and biomechanical data. Comparing their upper extremity to the human upper extremity can give insight into what morphological features are associated with the ability to perform overhead tasks and what concurrently evolved features are responsible for limiting human overhead capacity.

1.2 Morphological Comparative Approaches to Biomechanics

Anthropologists have been studying the comparative shoulder morphology of primates, ancient humans and modern humans for over a century (Larson & Stern, 2013). These analyses have mostly been morphological comparisons of specific boney features of interest. From these analyses, certain morphological traits have been identified as differentiating the human and chimpanzee shoulder. These include the length and width ratio of the scapular body, orientation of the scapular spine, orientation of the glenoid, the projection of the acromion, size of the humeral head, torsion of the humeral shaft, and insertion sites of the rotator cuff muscles and deltoid (Larson, 1998). How each of these morphological traits may or may not contribute to functional capacity is unknown. While helpful in understanding shape difference between species, comparative morphological analyses are incapable of determining the quantitative contribution of specific traits to function and how they relate to evolutionary changes in locomotor behaviors (Hutchinson, 2013). Methods that integrate musculoskeletal form and function would provide more quantitative answers.

The coordination of anthropological and biomechanical modeling techniques provides new revelations in human evolution and function. Musculoskeletal modeling offers a platform to integrate morphological knowledge from physical anthropology into advanced biomechanical methods to further our understanding of human evolution and modern human function. Musculoskeletal computational biomechanical models use information regarding bone shape and orientation, and soft tissue physiology, architecture and origin and insertion data to determine joint and soft tissue forces and moments during specific simulated tasks (Dickerson, 2008). These approaches can be used to quantify the musculoskeletal differences between the locomotor shoulder of the chimpanzee and the non-locomotor shoulder of the human while performing the same tasks. Further, probabilistic musculoskeletal models that alter specific morphological traits of anthropological interest can quantify the effect of these traits on joint biomechanics. Musculoskeletal models of the human shoulder exist, however no analogous models exist of the chimpanzee shoulder for comparative purpose.

1.3 Objectives and Thesis Outline

The purpose of this thesis was to provide an analysis of the musculoskeletal differences between the human and chimpanzee shoulder to provide evolutionary explanations for modern human shoulder function. The dissertation aimed to expand biomechanical research on modern human climbing abilities, and provide the first probabilistic model of a chimpanzee glenohumeral joint that considers anthropologically guided morphological variability. This novel model will be analogous to an existing human glenohumeral model, the Shoulder Loading Analysis Modules (SLAM). This proposed dissertation consisted of four linked studies (Figure 1). Overall, it was hypothesized that the experimental, modeling and probabilistic procedures would demonstrate the musculoskeletal deficiency of the modern human shoulder to engage in weight-bearing, overhead climbing behaviors, and identify specific evolved musculoskeletal differences between species that account for differences in overhead capacity.

Study 1 empirically measured the kinematics and muscular activity of humans performing a horizontal bimanual arm suspensory climbing task in experienced and inexperienced climbers. As well as providing data on human capabilities for brachiation, this data provided postural inputs to the operate the glenohumeral models for an overhead climbing simulation in Study 3 and Study 4. Study 2 focused on the development of geometric parameters necessary for the development of the chimpanzee glenohumeral model. First, the chimpanzee shoulder rhythm was created, using the x-ray data and structure of the human shoulder rhythm as a guide. Second the geometric constraint of glenohumeral dislocation ratios were developed by defining structural differences between chimpanzees and humans in glenoid depth. Study 3 compromised the building and running of the deterministic musculoskeletal chimpanzee glenohumeral model using sourced bone and muscle morphology data, the derived geometry parameters in Study 2, and modified kinematic data of chimpanzee climbing. Muscle force and subacromial space width were compared to those obtained from the human model. The fourth and ultimate study was the expansion of the human and chimpanzee models to probabilistic versions using known variable ranges of morphological features associated with anthropological adaptations. Study 4 considered the effect of evolutionarily relevant morphological feature distributions on rotator cuff muscle force predictions between species.

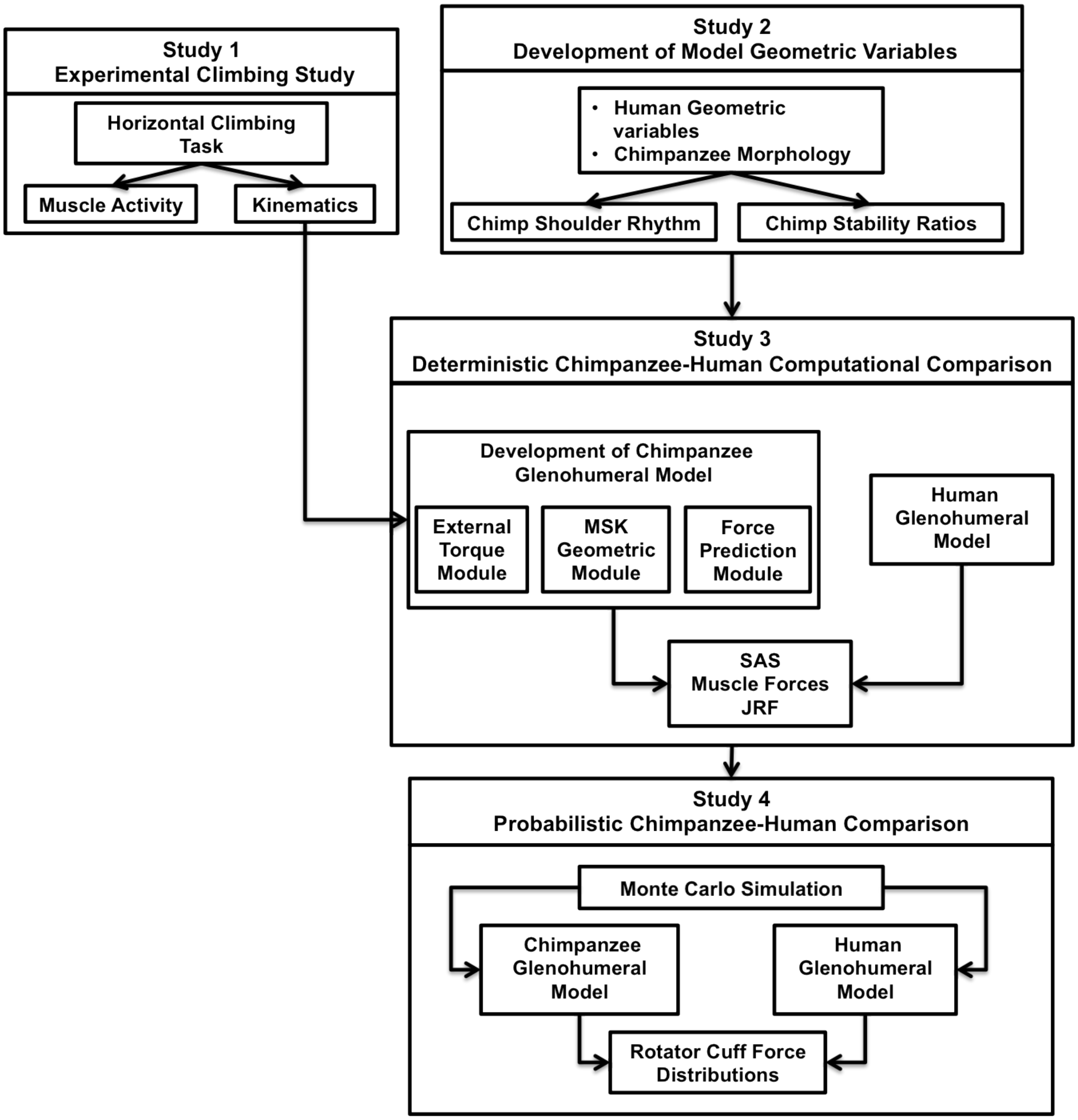


Figure 1: Flowchart representing the division of the four studies that comprise the thesis, and how they link to the overall goal of creating a probabilistic chimpanzee shoulder model for evaluating anthropological morphology associated with overhead posture capacity. Outputs for each study are in double-lined boxes. SAS = subacromial space. JRF = joint reaction force. MSK = musculoskeletal.

Chapter 2 Literature Review

There are still many questions about the evolutionary process that led to the present human physical form and ability. Fossilized evidence suggests that humans came from an arboreal, tree locomoting ancestor. By becoming habitual bipedal beings, the human shoulder complex altered to be less adapted for overhead postures. In return, humans became efficient hunters, swimmers and endurance bipeds. These behaviors are believed to have been integral to the survival and prosperity of the human species. The closest living relative to humans, the chimpanzee, has retained arboreal locomotor behavior. Studying the chimpanzee shoulder musculoskeletal morphology may provide information on what musculoskeletal traits are integral to arboreal and brachiating locomotion. Comparison of chimpanzee shoulder morphology to human will conversely also help identify what shoulder traits are associated with uniquely human upper extremity behaviors. This information could transfer to the morphological study of human fossilized remains by pin pointing how and when humans evolved certain locomotor behaviors.

Anthropological analyses isolate specific morphological traits for between and within species comparison. While useful, this does not merge shoulder morphology to demonstrate how musculoskeletal traits interact to meet behavioral demands. Biomechanical computational modeling offers a new approach to integrate species-unique musculoskeletal joint morphology to determine physical capability and function between species. Computational modeling can provide cohesive and integrated analyses of the shoulder morphology to anthropological study.

2.1 Human Evolutionary Tree

Genetic analyses have demonstrated the classification of the human species and relativity to other animals. Humans as a Species are classified as *Homo sapiens*, reflecting the Genus *Homo* to which they belong. The human tribe belongs to the Hominoid Family of the Order Primates in the Mammalia Class (Cartmill & Smith, 2009). Hominoid is also the Family that all great apes – *Pan* (chimpanzees and bonobos), *Gorilla* (Gorillas) and *Pongo* (Orangutans) (Figure 2) – and lesser apes such as gibbons belong (Young, 2003). Primates are a wide-ranging and varied order that encompasses over 200 species that have retained at least some arboreal behaviors (Cartmill & Smith, 2009). The closest living primate relatives to humans are chimpanzees, *Pan troglodytes* (Oxnard, 1969). Molecular genetic studies have demonstrated that humans and chimpanzees split to form their own evolutionary paths no more than 6.3 million years ago (Figure 2), and likely even more recently, less than 5.4 million years ago (Patterson et al., 2006). Following this, the human species began its own evolution to become the modern humans they are today.

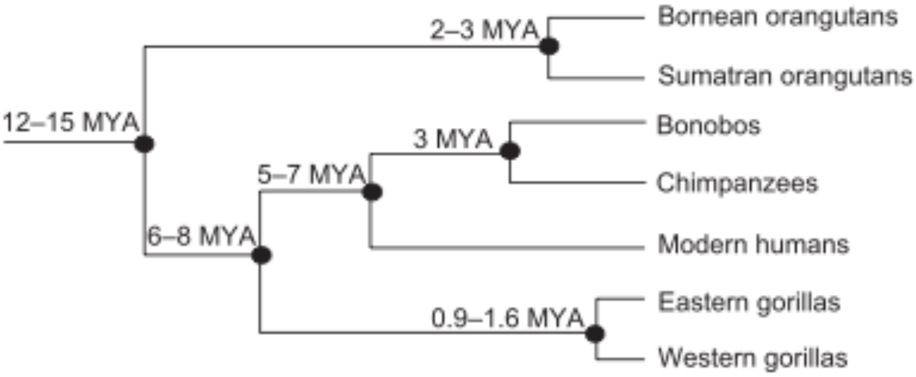


Figure 2: Estimated time of divergence among all extant hominoids. Humans and *Pan* (Chimpanzees and Bonobos) are estimated to have diverged between 5 and 7 million years ago (MYA) (Robson & Wood, 2008).

2.1.1 Fossilized Evidence of Human Evolution

The consensus human family tree adapts and refines based on new fossil finds and analyses of previously discovered fossils. Based on cranial morphological analyses, the human evolutionary tree following the human split with chimpanzees to the modern *Homo sapiens* is presently believed to be represented by Figure 3. Some of the oldest fossils of the human lineage are those that fall under what has been named the Ardipithecus (Ar.) family (Figure 3), dated to be approximately 5-7 million years old. One of the most well known subspecies is the Australopithecus family; specifically Australopithecus *afarensis*. Over one hundred specimens of this species have been found amid the East African Rift Valley. This includes the famous AL-288-1 fossil, colloquially known as Lucy, a nearly half complete adult female, bipedal skeleton (Wood, 2012). Most early hominins are confined in their distribution of fossilized remains, being geographically contained to Africa, and sheltered and protected areas near permanent water sources (Kimbel et al., 2009; Niemitz, 2010). The lower and upper limb proportions of many Ardipithecus and Australopithecus fossils have both chimpanzee and modern human morphological traits (Cartmill & Smith, 2009). The oldest hominin fossils of the Ardipithecus family, including *Ar. Ramidus*, *O. tugenensis* and *S. tchadensis*, show anatomical signs of bipedalism, and are the closest link to the human common ancestor with chimpanzees (Pickford & Senut, 2001; White et al., 2009; Wood & Lonergan, 2008).

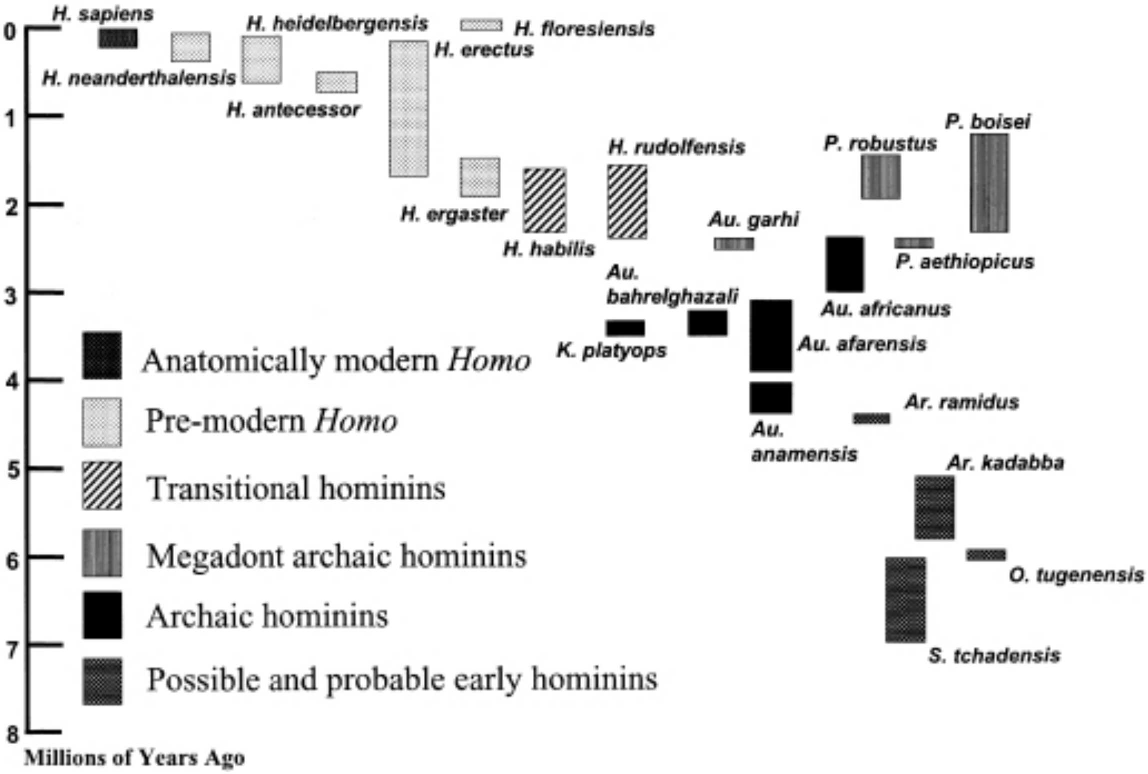


Figure 3: Hominini family tree, demonstrating the identified species of the human evolutionary tree, from the most ancient Australopithecines to modern *Homo sapiens* (Wood & Lonergan, 2008).

Eventually, a species of Australopithecus likely gave way to the species of *Homo* around 2 million years ago (Figure 3). The first fossils of *Homo* appeared in the fossil record approximately 1.8 million years ago, and are often designated *Homo erectus* (Wood, 2010). With the appearance of *Homo*, fossilized remains suggest that human ancestors began to spread more throughout Africa and into Eurasia for the first time. Many of the earliest non-African fossil remains of the *Homo* have been found in the eastern parts of Europe, and western Asia. By approximately 400,000 years ago, the *Homo species* was all across Eurasia (Anton, 2003; Cartmill & Smith, 2009). The expansion of hominins into Eurasia brought what appears to be much variation in hominins and advancements in human evolution that encompass the Middle Pleistocene era. Early *Homo* species demonstrate more modern human hand bones, which exhibit features associated with the ability for precision grip (Tocheri et al., 2007; Wood, 2010). Combined with a larger brain, the human-like hands suggested the ability to use and manipulate tools. This is confirmed by the discovery of stone tools with the fossilized remains.

2.2 Evolution of the Upper Extremity

The pectoral girdles of land vertebrates have a similar general structure, but with distinct features for specialized locomotor usage of the lower and upper extremities, respectively (Starck, 1979). Both the pelvic and pectoral girdles function as sturdy connections between the vertebral column, and the upper and lower extremities. Both extremities have substantial mobility, aided by the stable frame of the trunk, and pelvic and pectoral girdles, and the large muscles that originate from them (Alexander, 1981). The lower extremity is generally used more in locomotion, by bearing more of the body mass and propelling the body forward (Alexander, 1981). Consequently, the lower extremity usually has more massive musculature, and possesses less degrees of freedom and mobility (Alexander, 1981). The upper extremity tends to have more variable functional abilities, which can often be useful in the characterization of a species (Young, 2006). These functions include running, flying, swimming, climbing, crabbing, digging, and grasping (Pronk, 1991). Depending on the functions of the pectoral girdle, its structure can vary from a firm and stable one in committed terrestrial quadrupeds like felines and canines, to a more mobile one found in primates (Veeger & van der Helm, 2007). The variable specialties of the upper extremity make it useful to examine for the purpose of comparative functional anatomy.

Primates share a similar pectoral girdle morphology. The basic formation of the pectoral girdle includes the seven bones of the sternum, the clavicle, the interclavicle, the (meta)coracoid, the scapula, and the cleithrum (Pronk, 1991). The functional behaviors of a species alter the development (and existence) of these bones, correlating upper extremity musculoskeletal structure with function (Oxnard, 1969). Humans and other primates have a sternum, clavicle, and scapula (Romer et al., 1974). Other bones of the girdle have merged into these three bones. The scapula can be considered the most important bone in the upper extremity, as it is a large muscle attachment site for the upper extremity and well as muscles connecting the scapula to the thorax (Lugo et al., 2008). In general, all Hominoid primates, including humans, can perform similar modes of locomotion and activities with their lower and upper extremities, including bipedalism, quadrupedalism, and climbing. Thus, Hominoids share very similar pectoral girdle morphology. However, the biomechanically different requirements of each locomotor task and the degree to which it is performed are reflected by unique characteristics of the upper extremity of each Hominoid species.

Given the correlation between upper extremity form and function, it is believed that small evolutionary morphological adaptations of the shape and structure of the pectoral girdle have altered the functional capabilities of the shoulder (Oxnard, 1969; Wang et al., 2004). Evolution of the human upper extremity is influenced by many factors, including environmental, dietary and phylogenetic (Wang et al., 2004; Richmond et al., 2001). These factors are likely to exert different influences throughout the evolutionary timeline, as the physical environment adapted as primates adapted as well (Wang et al., 2004). The human upper extremity is postulated to exhibit mobility due to its non-weight-bearing function in locomotion, and use in tactile, manipulatory and communicative behaviors (Oxnard, 1969). The manner and time course over which the upper extremity structurally evolved to allow these functions is not clear. High variability in fossils, holes in evolutionary timelines, impartial bones and the difficulty associating bone form with physical function make definitive inferences regarding the morphological adaptations of the shoulder difficult.

2.2.1 Evolutionary Changes in Human Locomotion

Humans are believed to have evolved from a terrestrial quadrupedal or arboreal common ancestor with chimpanzees into the modern bipedal species of today (Cartmill & Smith, 2009). Humans are the only mammals to habitually stride biped (Alexander, 1976). Birds perform a habitual biped gait when on terrestrial ground, however it is derived from a dinosaur lineage (Alexander, 2004) and is fundamentally different from human gait (Neimitz, 2004). Other mammals, including apes, occasionally walk bipedally and can only do so for limited distances (Napier & Napier, 1967). Walking biped requires that the center of gravity remain within the base of support of only the hindlimbs in order to stay balanced. Humans achieve this through evolutionary morphological adaptations, particularly in the feet, legs, pelvis, and vertebral column (Wood, 2010). Indirect morphological evidence for bipedalism, such as position of the foramen magnum and shape of the femoral neck and foot phalanx, found in the Ardipithecus family of possible hominins date as early as 6.5 million years ago (Wood & Lonergan, 2008), Fossilized remains of bipedal hominin footprints lend direct evident that humans were walking bipedally as much as 3.6 million years ago (Raichlen et al., 2010).

Anthropologists are uncertain about the purpose of the evolutionary adaptation towards bipedalism in humans. Most other animals that evolved to become biped did so to run faster (Alexander, 2004). This is not the case for humans (Bramble & Leiberman, 2004; Niemitz, 2004). Many proposed theories exist to explain bipedalism, including freeing of the upper extremity for non-locomotor jobs (Cartmill & Smith, 2009). Based on location of fossilized remains and geological exploration, humans are believed to have developed bipedal locomotion in a humid forested landscape (Haile-Selassie, 2001; Senut & Pickford, 2004). In such an environmental scenario, humans had easy access to nearby bodies of water, where rich food sources could be found through walking and wading in water (Niemitz, 2010). Safety was maintained by the proximity of nearby trees canopies (Niemitz, 2010).

Bipedalism serves a number of purposes in modern human behavior and biology. It allows humans to carry, throw, swing weapons, run long distances, swim better than other hominins, gesture with both hands, and see farther than they could when quadruped. It is likely that the advent of bipediality in humans served a combination of these benefits, and possibly others (Cartmill & Smith, 2009).

2.2.2 Evolution of a Non-Locomotor Upper Extremity

Bipedalism freed the upper extremity for a myriad of non-locomotor tasks that have aided in the survival and development of the human species. The ability to throw – in particular long-range projectile throwing – changed the behavior and lifestyle of archaic humans and is believed to be one of the most important human upper extremity adaptations (Roach et al., 2013). The ability to throw changed human predatory behavior, subsistence strategies and competitive interactions between different groups of humans by changing the type of prey humans could target and where they could hunt (Churchill & Rhodes, 2009; Marlow, 2005). Further, long-range throwing allowed human hunting and travel in what was typically considered less safe open country (Churchill & Rhodes, 2009). Not only were new food and nutrients now available to humans, but throwing also changed human interaction. It introduced a new threat of violence and altered interpersonal agonism, coercion, coalitions and violence (Bingham, 2000). The ability to throw had a clear effect of the evolution of human physicality and behavior.

When long-range throwing adaptations occurred is still debated. The earliest stone tools appear approximately 2.6 million years ago in Ethiopia. These tools appear to be Oldowan choppers, scrapers and flakes, likely used by a species of *Australopithecus* (Cartmill & Smith, 2009). It is possible tools were used earlier, but were made from perishable or natural, unmodified materials like bones, branches and sticks that remained unidentifiable as part of the archeological record (Cartmill & Smith, 2009). Remains of man-made spears used for some forms of hunting have been discovered as far back as 400,000 years. Some of these tools have been for close range (hand-deployed) spear throwing, while others are believed to have been used for long-range spear throwing projectiles and darts of up to 40m or more (Churchill, 1993; Churchill & Rhodes, 2009). Analysis of archeological evidence of spears and darts has lead researchers to believe that humans began developing long-range projectile weaponry in Africa sometime between 90,000-70,000 years ago (Churchill & Rhodes, 2009).

The use of the upper extremity for such non-locomotor purposes such as long-range throwing has led some to believe that the upper extremity is what provided the means for human evolution, both physically and intellectually (Roach et al., 2013). With the unique ability to throw at high speed, ancient humans were able to hunt bigger game and eat more nutritious, protein rich food (Churchill & Rhodes, 2009). This may have been an important factor in the enlargement of the human brain size approximately 400,000 years ago (Cartmill & Smith, 2009; Roach et al., 2013). Throwing also provided a means for the slow and weak human species to protect themselves, and make the movement beyond safe havens possible, enabling migration, settlements and eventually modern societies.

2.3 Modern Human Shoulder Capabilities

Owing to its non-locomotor usage, the modern human shoulder is highly mobile and unstable, with a large range of motion. From an anatomical position, an average adult human can flex and extend their arm in the sagittal plane nearly 160° and 55°, respectively, abduct their arm 170° and adduct 50°, and horizontally flex and extend the arm 135° and 45° in the transverse plane (American Academy of Orthopaedic Surgeons, 1965). This range allows for overhead postures, though not for locomotor purposes like other primates. Other closely related primates perform arboreal locomotion, swinging and climbing from tree branches, while modern humans, as habitual bipeds, stay on terrestrial ground (Bertram & Chang, 2001; Usherwood et al., 2003).

The large range of motion at the human shoulder gives humans the ability to perform numerous upper extremity tasks that are integral to their current physical and social behaviors. This includes the ability to throw long range and at high speeds, both overhead and underhand (Churchill & Rhodes, 2009). The large range of flexion and extension provides the ability to swing the arm during walking and running, giving humans the balance needed to be effective long distance travelers (Bramble & Lieberman, 2004). Horizontal adduction, adduction and flexion give humans the ability to bring their arms and hands in front of their body, making humans capable of carrying infants and other objects, from wood for a fire to a glass of water, and even hugging. Combined with the fine motor control of the hand, the mobile shoulder also allows for tool manipulation. This includes large-scale work such as building homes, and fine control tasks like needlework. With regard to the strong development of human social behaviors, the large range of motion at the shoulder has brought about language and communication in the form of writing, typing, drawing, music and hand gestures. The shoulder also allows humans to engage others simultaneously using both eye gaze and hand gestures while we speak, which has been important to social development and communication.

2.3.1 Humans Performing Overhead Tasks

The overhead postures that may have once been linked to the human ability to brachiate are problematic to modern humans. Sustained and repetitive overhead postures lead to fatigue of the shoulder muscles (Ebaugh et al., 2006; Rashedi et al., 2014). Muscle fatigue caused by overhead postures has been implicated in the development of kinematic changes, pain, soft tissue injuries and joint disorders (Chopp et al., 2010; Cote & Bement, 2010; Marras et al., 2006; Stauber, 2004). The infraspinatus and deltoid muscles demonstrate particularly high levels of fatigue following an arm elevation fatigue protocol, but the trapezius and serratus anterior muscles also become fatigued (Ebaugh et al., 2006). Especially problematic is the change in kinematics that coincides with fatigue of the shoulder musculature. When the arm is elevated, the scapula goes through predictable three-dimensional rotations of upward rotation, posterior tilt and external rotation. The clavicle elevates and retracts and the humerus elevates and externally rotates (Ebaugh et al., 2006; McClure et al., 2001; Ludewig & Cook, 2000). Once fatigue of the shoulder musculature sets in, these kinematic motions become altered. The scapula increases in upward rotation and external rotation (Chopp et al., 2011; Ebaugh et al., 2006). The humerus also has decreased external rotation and the clavicle retracts less in arm elevation (Ebaugh et al., 2006). Fatigue of the rotator cuff muscles in sustained overhead postures cause them to be unable perform the role of countering the superior pull of the active deltoid muscle, and thus fail to maintain a humeral head position that is centered in the glenoid (Chopp et a., 2010). As a result, the humeral head migrates superiorly, decreasing the subacromial space (Chopp et al., 2010). The combination of these kinematic changes may cause decreases in the subacromial space and consequently impingement of tissues (Lewis et al., 2001).

Evolutionary modifications of the human upper extremity have made it less adapted to overhead postures. Ancient humans have a cone-shaped thorax that is more similar to modern chimpanzees, the closest living human relative (Figure 4), which places the scapula in a position of greater upward rotation, and a glenoid fossa that is angled more superiorly relative to the scapular body (Schmid, 1983; Stern & Susman, 1983). The modern human glenoid fossa faces medially, creating a medial, not cranial, facing glenohumeral joint (Green, 2013; Larson et al., 2007). The acromion of the modern human scapula faces laterally over the glenoid fossa (Figure 5). In all the great apes, the acromion is oriented superiorly and less laterally to the glenoid fossa, (Figure 5) providing more space between the acromion and the glenoid (Oxnard, 1984). Both of these features are ideal for overhead behaviors, and are absent in modern humans (Lewis et al., 2001). Modern humans have a shorter forearm than chimpanzees and ancient humans, which reduces the leverage and reach for swinging during brachiation (Lewis et al., 2001). These skeletal adaptations in modern humans reduced the subacromial space and oriented the shoulder for efficiency in arm postures below 90° (Lewis et al., 2001). This consequently lessened the human capacity for overhead behaviors, including the brachiation that may be an ancestral behavior to modern humans.

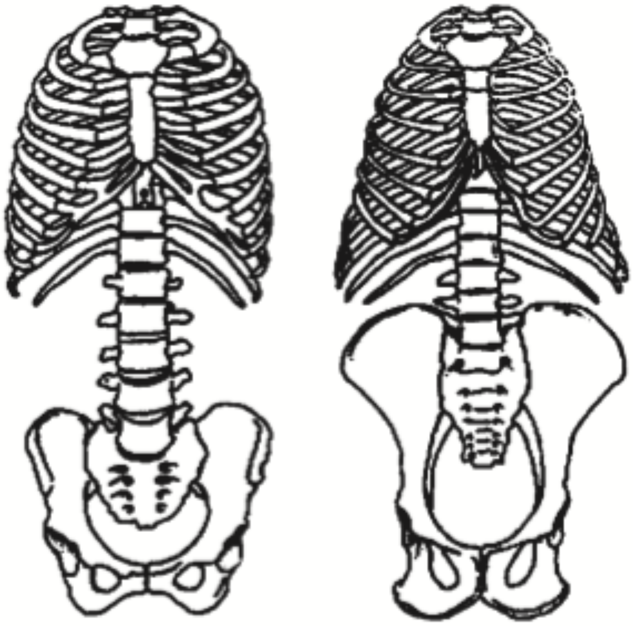


Figure 4: The shape of the human (left) and primate (right) thorax changes the orientation of the scapula. The cone shape of the primate orients the scapula in more upward rotation (adapted from Lewis et al., 2001).

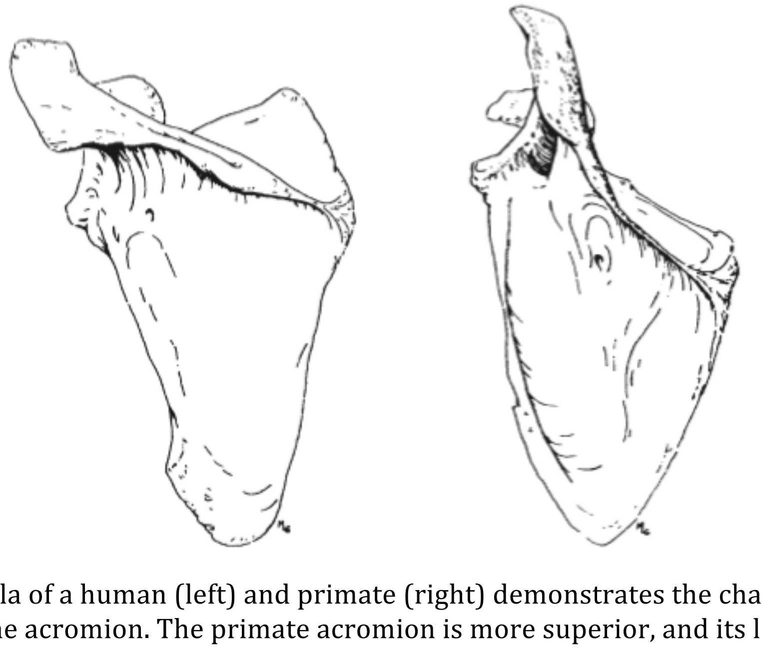


Figure 5: Scapula of a human (left) and primate (right) demonstrates the change in orientation of the acromion. The primate acromion is more superior, and its less lateral

position provides less superior coverage of the glenoid fossa than in humans (Lewis et al., 2001, Oxnard, 1984).

The human upper extremity musculature has also adapted to produce speed and precision, as opposed to the chimpanzee upper extremity that is designed for strength and power (Walker, 2009). When normalized for size, the chimpanzee can produce four times as much force in a one-handed pull than a human (Bauman, 1923, 1926). The musculature of the human shoulder has adapted for less strenuous non-locomotor tasks, demonstrating a reduced muscle mass compared to the great apes (Larson & Stern, 2013; Lewis et al., 2001). Chimpanzees have approximately 16% of their total body mass in the upper extremity, while humans have less than 10% (Zihlman, 1992; Walker, 2009). Serratus anterior and upper trapezius are two muscles responsible for upward rotation of the scapula (Lewis et al., 2001). Owing to the oblique orientation of the medial border to the elongated scapular spine, this muscular couple is more cranially oriented, and much more developed in arboreal primates to aid in scapular rotation during brachiating activities (Green, 2013). In modern humans, the orientation of these muscles is more similar to those of habitual quadruped primates and not the great apes (Oxnard, 1967). The more perpendicular angular relationship between the medial border and the scapular spine in quadrupedal primates causes the trapezius to be a scapular retractor (Ashton & Oxnard, 1964; Green, 2013). The supraspinatus fossa is also smaller in humans than in the great apes, implicating the supraspinatus as a smaller muscle and weaker arm elevator (Lewis et al., 2001). Combined with lower muscle mass, this means the human shoulder musculature is likely not capable of sustaining activity in overhead postures.

2.3.2 The Loss of Human Arboreal and Overhead Capacity

Limited capacity in overhead postures in humans is surprising, given the likelihood of an arboreal ancestry. The bone shape of fossilized remains of ancient humans share many traits with the chimpanzees and arboreal primates. Morphological traits such as a cone-shaped thorax, elongated scapula, less laterally projected acromion and superiorly oriented glenoid have all been discovered on ancient humans (Lewis et al., 2001; Young et al., 2015). These traits are advantageous for arboreal locomotion. Ancient human fossils also have a robust humerus, much like chimpanzees (Ruff et al., 1993; Walker, 2009). This is telling, as it implicates high stress on the upper extremity that likely occurred during locomotor behaviors. These musculoskeletal features are no longer present in modern humans. Humans appear to have devolved arboreal, overhead postural abilities. This is not true of chimpanzees who spend a great deal of time in overhead postures, brachiating through the forest trees with little risk of injury due to fatigue (Stern & Larson, 2013). Chimpanzees have maintained a shoulder with powerful musculature and boney orientations that encourage overhead postures. While there are theories as to how the devolvement in humans occurred, pinpointing the musculoskeletal factors that most affect the human limited ability to perform overhead postures is debatable and often confusing (Young, 2003, 2005, 2008). Chimpanzees represent a living example of a closely related hybrid arboreal and terrestrial musculoskeletal upper extremity system. What differentiates the human and chimpanzee shoulder in terms of physical overhead capability is uncertain. Developing robust answers requires a quantified and integrated analysis and comparison between the human and chimpanzee shoulder musculoskeletal system.

2.3.2.1 Human Rotator Cuff Evolution

Human shoulder musculature, particularly the rotator cuff, is partially the result of a common evolutionary path with chimpanzees, and a sign of shared ancestral locomotion. Though still debated, humans are believed to come from an arboreal, climbing ancestor. Primates likely evolved their unique shoulder and rotator cuff as a survival mechanism to arboreal habitats (Tuttle, 1969). A true rotator cuff is the blending of the tendons of the supraspinatus, infraspinatus and teres minor into a single insertion onto the greater tuberosity of the humerus and is considered rare (Sonnabend & Young, 2009). The presence of a rotator cuff is associated with habitual use of the upper extremity beyond the sagittal plane, extreme glenohumeral mobility – particularly in overhead brachiating postures – and the need for high muscular stability (Roberts, 1974; Sonnabend & Young, 2009). The existence of a true rotator cuff in humans represents a common ancient adaption with chimpanzees and orangutans for more glenohumeral mobility and overhead postures for locomotion in arboreal habitats (Fleagle, 1999; Tuttle, 1969). Yet, compared to other primates, modern humans have a smaller, weaker rotator cuff adapted to non-locomotor, repetitive, low-cost behaviors that can become easily fatigued (Ebaugh et al., 2006; Lewis et al., 2001; O'Neill et al., 2017). While the present human morphology of the rotator cuff is less suited to climbing, its existence may be the result of an evolutionary holdover from arboreal locomotion.

2.4 Chimpanzees –Closest Living Human Relative

2.4.1 Chimpanzees (*Pan Troglodytes*)

Research has strongly demonstrated the physical, behavioral and genetic evolutionary connection humans have with chimpanzees. As the closest genetic relative to humans in the animal kingdom, the endangered chimpanzee (*Pan*) is a member of the Hominoid family and the sister taxa to humans (Oxnard, 1969). Chimpanzees share between 94-98% of their DNA with humans (Cartmill & Smith, 2009). Smaller than humans, chimpanzees weigh between 32 and 60 kilograms, and can stand at approximately 1.2-1.7 meters, a height owed largely to their elongated limbs (World Wildlife Fund, 2015). Chimpanzees live up to approximately 60 years in the wild (World Wildlife Fund, 2015). Based on geographic region, there are three identified chimpanzee subspecies (Zihlman et al., 2008). The degree of genetic variation between subspecies of chimpanzees is comparable to that seen in humans, suggesting that they do not represent distinct species, but normal variation within a single species (Fischer et al., 2006).

Chimpanzees reside in a variety of habitats, including forest, savanna and woodland and exhibit a variety of behaviors. The divergence of behaviors in chimpanzees is dependent on their ecological habitat. Chimpanzees are highly intelligent, using tools such as reshaped sticks and rocks to obtain food, and even hunting co-operatively. Like humans, chimpanzees eat with their hands and can throw, but not with the same speed or accuracy (Roach et al., 2013; World Wildlife Fund, 2015).

Those that live in forests typically use more tools and make them in more varied ways, and hunt more frequently and cooperate more often for hunting purposes (Uchida, 1996).

Chimpanzees engage in a number of different forms of locomotion, and their physical form demonstrates a compromise to accommodate this variety. Chimpanzees spend the much of their time on terrestrial ground, walking quadrupedally. They also spend a significant amount of time in trees, where they swing, cling, forage and sleep (World Wildlife Fund, 2015). Chimpanzees can also walk bipedally, but only out of necessity and for little more than one kilometer at a time (World Wildlife Fund, 2015).

If the common ancestor between chimpanzees and humans was arboreal, as has been suggested, two distinct shoulder morphologies arose from this parent species. One rose to develop the modern chimpanzee shoulder, capable of brachiation and terrestrial quadrupedialism. The other gave rise to the bipedal modern human shoulder: mobile, flexible and non-weight-bearing (Oxnard, 1969). This evolutionary pathway would have forged the loss of suspensory, overhead capabilities in human ancestors as a means for greater bipedal terrestrial endurance and tool manipulation capacity (Bramble & Lieberman, 2004; Oxnard, 1969). In turn, chimpanzees may have gained terrestrial quadrupedal capabilities while retaining arboreal capabilities for brachiation (Oxnard, 1969). These distinct evolutionary differences between species have been a source of interest for scientists for many years, bringing about much study of the chimpanzee species.

2.5 Difficulties with the Study of Primate Biomechanics

Studying primate biomechanics suffers from similar limitations to biomechanical studies on humans. Most studies must occur in a controlled laboratory setting, as attempting to capture kinematics, kinetics and muscle activity in a natural setting is very difficult (Stevens & Carlson, 2008). Laboratory settings allow for control of environmental factors so that specific biomechanical variables of interest can be studied in isolation. However, a laboratory setting is often small and confined, and cannot replicate some of the complexities of a natural setting, limiting the generalization of findings (Stevens & Carlson, 2008). With respect to brachiation, a constructed laboratory arboreal setting will likely lack the variability and complexity of natural forest canopies.

Captive animals that are used in laboratory settings are often physiologically, biomechanically and behaviorally different from their wild peers. Captive animals receive medical care, and are accordingly in better health, and can even have different skeletal morphology than wild animals (Sarmiento, 1985). Biomechanical study of non-human animals also suffers from behavioral constraints of the subject (Stevens & Carlson, 2008). Captive animals often lack motivation to perform typical natural behaviors, as they lack the motivators present in a natural setting, and thus are often less active than wild animals (Stevens & Carlson, 2008).

Animals are less compliant than human subjects. Getting a chimpanzee to perform a simple task requires patience as the research team waits for the desired task to be completed successfully by the subject. Further, animal subjects may interfere with protocols, including pulling off and damaging equipment like as motion capture markers and electrodes. Resultantly, researchers in the field of primate biomechanics follow different procedures than in human biomechanics to avoid these problems. These adaptations include subject sedation to insert indwelling electrodes, use of painted on markers, simplified marker set-ups and minimizing the number of markers and electrodes used (Demes & Carlson, 2009; Schmidt, 2005; Usherwood et al., 2003). While these experimental adaptations may signify the loss of biomechanical data, it is at present the only manner in which quantitative biomechanical information can be collected on primates. Though less precise and detailed as biomechanical data on humans, these studies provide important information regarding the gross biomechanics of movement in primates.

Another issue in animal experimental settings is subject availability. While chimpanzees are often of paramount interest to researchers examining human evolutionary adaptations, they are scarce due to species endangerment. Other primates, such as gibbons and spider monkeys, have provided a useful alternate model for brachiation behaviors in primates. Chimpanzees, gibbons and even spider monkeys share a large portion of shoulder musculoskeletal morphology, owing to similar physical behaviors and functional contributions of the shoulder to locomotion and voluntary movements (Larson, 1988).

Despite these limitations, laboratory experiments offer the ability to study animals in a highly controlled manner. The tasks performed and the environment on which they are performed are pre-determined and adjusted to answer specific biomechanical questions. Though requiring patience, adherence to proper protocols ensures successful acquisition of the desired data. The quantified data obtained in laboratory studies cannot be matched in a natural setting (Stevens & Carlson, 2008).

2.6 Primate Locomotion

The chimpanzee ability to perform arboreal and terrestrial locomotion has created an upper extremity that is a morphological hybrid of obligate terrestrial quadrupeds and arborealists. That is, the chimpanzee musculoskeletal system is not optimized for either behavior, but is a compromise to afford both arboreal and terrestrial locomotion (Rose, 1991). Data on the time chimpanzees spend on ground and in trees during waking hours varies from study to study (Doran, 1996). Some populations have been shown to spend a greater time in arboreal settings, while others spend the majority of their time on the ground (Takemoto, 2004). These decisions are hypothesized to be reliant on environmental factors such as whether it is a dry or wet season, with arboreal time increasing during the wet seasons to control thermoregulation (Takemoto, 2004). Much of the chimpanzee's arboreal time is spend in more sedentary behaviors, with interspersed brachiating and climbing (Takemoto, 2004). Arboreal behaviors allow chimpanzees to obtain food sources, maneuver within the forest canopies, and avoid prey (Pontzer & Wrangham, 2004). Chimpanzees often travel terrestrially up to 5 kilometers per day (Chapman & Chapman, 2000; Wrangham, 1977). This behavior is energetically costly and slow (Pontzer & Wrangham, 2004), though often necessary to travel between food patches (Chapman & Chapman, 2000). The upper extremity of the great apes appear to be mostly adapted to arboreal activities, with secondary adaptions for quadrupedal walking (Larson & Stern, 1987). To allow both forms of locomotion, some features in the forearm long bones, and hand have adapted to accommodate multiple forms of locomotion (Pontzer & Wrangham, 2004).

Primates have adapted to be able to reach out precisely and securely to grab branches or objects. This precision for reaching, foraging and manipulation is afforded by greater supraspinal cortical control of upper extremity movements (Georgopolous & Grillner, 1989; Larson et al., 2000). The ability to reach also requires increased mobility and subsequent increased range of motion of the upper extremity, especially at the shoulder. This increased mobility required for arboreal precision activities comes at a price. Increased joint mobility decreases joint stability (Larson, 1998). A mobile joint cannot endure high levels of force, especially during locomotion, or it will become destabilized (Larson, 1998). As a result of the less stable upper extremity, the primate lower extremity provides the majority of support and propulsive force during chimpanzee quadruped gait (Larson, 1987, 1998).

The uniquely elongated primate upper extremity that maintains grasping capabilities may have evolved to allow reaching in small-branch settings (Larson et al., 2000). Limb elongation in other mammals who are limited to terrestrial locomotion occurs to reduce the inertial properties of the limb, allowing bones to become longer and thinner, shifting mass proximally (Hildebrand, 1988). This makes it easier to swing the limbs, increasing running efficiency and maximal ground speed (Hildebrand, 1988; Larson et al., 2000). However, this reasoning does not hold for primates. Chimpanzee terrestrial locomotion is energetically higher than that observed in other mammals (Pontzer et al., 2014; Sockol et al., 2007). Instead, a suggested evolutionary pathway for primate upper extremity limb elongation is precision control needed for securing gripping of branches and objects in an arboreal setting. The mobile primate upper extremity requires a compliant (less stiff) gait pattern in arboreal settings (Larson et al., 2000). As cortical control of the upper extremity increased, fine motor control in the hand increased. This improved manipulatory and foraging abilities, which led to greater range of motion and joint mobility. Stability of the upper extemity joints became somewhat compromised, and primates were forced to adopt more cautious quadrupedal locomotor behaviors to less ground reaction forces during gait (Larson et al., 2001).

2.6.1 Primate Quadrupedalism

Chimpanzees, as well as gorillas, walk quadrupedally in a unique manner called knuckle-walking (Kivell & Schmitt, 2009). Typical mammalian quadrupedalism involves palm contact on all four limbs with the ground (English, 1978). Chimpanzees flex the fingers of the upper extremity toward the palm and weight-bear on the knuckles instead of the palm (Figure 6). The chimpanzee elbow and wrist remain quite stable during quadrupedalism, with no more than 10° of motion in a gait cycle, while the shoulder goes through 40° of swing (Pontzer et al., 2014). This form of locomotion is necessary as arboreal animals have long carpal bones for climbing and grasping behaviors. Walking on the knuckles protects the carpals from injury that could hinder other forms of locomotion and feeding behaviors (Kivell & Schmitt, 2009; Wood, 2010). However, owing to their elongated limbs, chimpanzee knuckle-walking causes an overstride gait. Overstride occurs when the placement of the hindlimb is over or in front of the preceding footprint of the forefoot (Larson et al., 2000; Larson & Stern, 1987). To complete the overstride, the chimpanzee's trunk angles laterally as the hindfoot passes to one side – either inside or outside – of its ipsilateral forefoot (Larson & Stern, 1987).

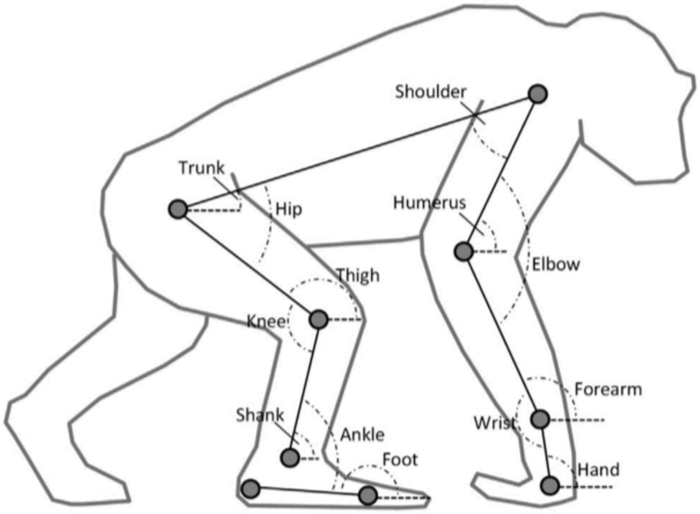


Figure 6: Sagittal view of chimpanzee knuckle-walking quadrupedalism. The palm of the hand in flexed, folding the fingers in, so the chimpanzee walks on the knuckles (from Pontzer et al., 2014).

The awkward knuckle-walking gait is likely a compromise to accommodate both arboreal and terrestrial locomotion, and to maintain adequate speed at low stride frequencies (Larson et al., 2000). Terrestrial gait must accommodate musculoskeletal adaptations for arborealism, such as long grasping fingers and elongated limbs. Further, in an arboreal setting, a longer stride length is a more effective way of increasing speed when locomoting on tree branches (Demes et al., 1990). Tree branches can experience significant sway and potential breakage when high impact forces are exerted on their surfaces from locomoting primates (Demes et al., 1990). This sway is energetically costly for the primates, potentially dangerous, and can alert predators and prey to their presence (Larson et al., 2000). Minimizing the number of contact impacts through increased stride length increases the effectiveness of arboreal quadrupedal locomotion (Larson et al., 2000).

2.6.2 Primate Bipedalism

Like humans, chimpanzees also walk bipedally. Chimpanzees are facultative bipeds, typically walking on two limbs out of necessity for carrying food, infants or tools (O'Neill et al., 2013). The common human and chimpanzee ancestry means that the forms of bipedalism seen in both species may also have a common origin, but this is highly debatable (Cartmill & Smith, 2009). Chimpanzees have a distally oriented ishia that reduces the ability of the hamstrings to produce an extensor moment when the femur is extended relative to the pelvis (Robinson, 1972). This anatomical difference forces chimpanzees to maintain both a knee and hip that is flexed at all times throughout the gait cycle (Figure 7) (Sockol et al., 2007). Chimpanzees do not have similar gluteal placement as humans, and are forced to recruit the trunk musculature to control mediolateral sway (Shapiro & Jungers, 1994). By recruiting trunk musculature, experience large medial-lateral sway of the center of mass and challenges controlling balance in bipedal gait (Pontzer et al., 2014).

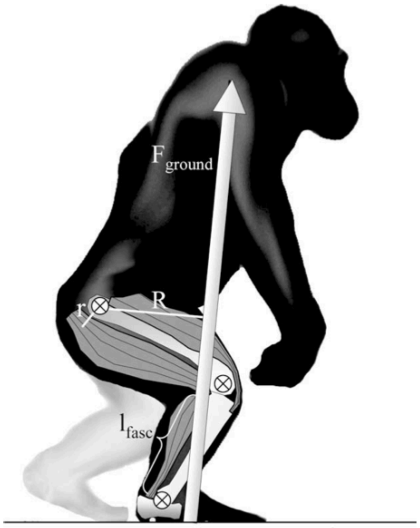


Figure 7: Example of the bipedal chimpanzee bent-knee, bent-hip gait. Note simple marker set-up of single markers on the joint centers (Pontzer et al., 2009).

While kinematically different from human bipedalism, chimpanzee bipedalism is often believed to be representative of a somewhat primitive form of human bipedalism (Pontzer et al., 2014). The cost of locomotion would have a great effect on natural selection and the adaption to habitual bipedalism in humans (Carey & Crompton, 2005). Efficiency of bipedalism, metabolically and otherwise, would have played a strong role in the selection for locomotion (Carey & Crompton, 2005). Compared to human bipedalism, chimpanzee bipedal gait produces greater ground reaction forces, and hip and knee moments when walking at similar speeds and is energetically more costly by as much as 50-75% (Carey & Crompton, 2005; Sockol et al., 2007). It is possible that this costly compliant, flexed limb (bent-knee, bent-hip) terrestrial gait in primates is due to a mechanical compromise that allows for greater locomotor variety, but less efficiency (Pontzer et al., 2009). However, the metabolic cost of bipedal and quadrupedal walking in chimpanzees is similar (Pontzer et al., 2014; Sockol et al., 2007). This implies that the cost of the human transition to bipedalism on the ground may have been low for early hominins, giving reason for the selection of bipedalism in early hominins (Pontzer et al., 2014).

2.6.3 Primate Brachiation Locomotion

Like terrestrial gait, primate brachiation (arm-swinging) follows kinematic patterns and cycles. At the beginning of swing phase, upon initial contact with the support, the arm is forced into extreme external rotation (Larson, 1988; Larson & Stern, 2013). At initial support contact, the body and arm are in a near-horizontal position. In mid-swing the body and arm swings underneath the support arm to become vertical and the body rotates axially about the shoulder thorough internal rotation of the arm and hypersupination of the support arm (Figure 8) (Larson, 1988; Larson & Stern, 2013; Usherwood et al., 2003). The rotation of the trunk brings the contralateral arm in line to create a double-support phase immediately before the original support limb releases (Larson, 1988). Prior to release of the ipsilateral arm from the support, the contralateral arm is near horizontal again as it reaches for the support, while the body begins to swing into a more horizontal position to propel forward swing (Usherwood et al., 2003). Elevation of the body occurs following mid-swing to increase reach range for contralateral support contact (Larson & Stern, 2013). The legs are typically bent throughout brachiation, increasing in mid-swing, but extending more as contralateral contact is made (Figure 8). In mid-swing the leg flexion can reduce the moment of inertia, while the leg extension at contralateral contact increases forward swing and helps propel the body forward (Usherwood et al., 2003). Upon release following mid-swing, the now non-support arm returns to anatomical position by mid-swing, but then begins the rotation toward support contact through arm external rotation and forearm hypersupination (Larson, 1988). The rotations of the arm and forearm are necessary to allow the trunk to rotate through 180 degrees of rotation to brachiate (Figure 8) (Larson, 1988). This extreme hypersupination is possible in primates, and particularly the gibbons, due to scapular orientation and the resulting low torsion of the humerus that repositions the elbow orientation (Larson, 1988). The human inability to hypersupinate to such a degree as other primates might be a limiting factor in human brachiation.

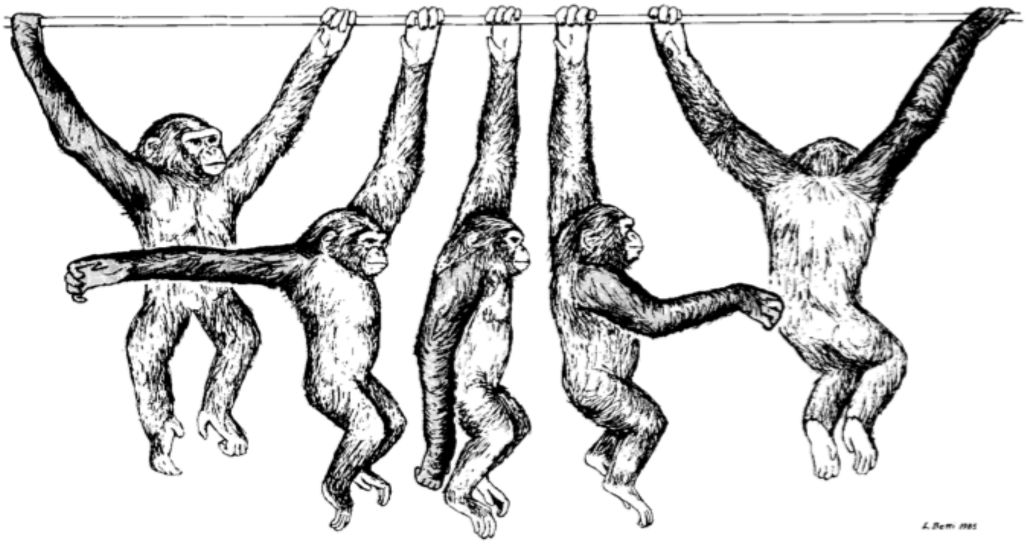


Figure 8: Chimpanzee pendular swing (no flight phase) recreated from video recordings (Larson, 1988). Axial rotations of the trunk, arm and forearm are what allow contralateral arm contact with the support.

As primates change the speed of brachiation, the mechanics of the locomotion changes as well. Brachiation speeds are determined by the spacing of branches and other supports (Bertram & Chang, 2001). Slow to moderate-speed brachiation behaviors in gibbons have been shown to somewhat mimic gait, by using a continuous contact brachiation where at least one hand is always in contact with the supporting branch throughout the entire swing cycle (Chang et al., 2000; Usherwood et al., 2003). The trunk and legs swing in unison with the support arm at slow- to moderate-speed brachiation (Bertram & Chang, 2001). This has been described as pendulum-like exchange of energy, much like in human gait (Chang et al., 2000). In high-speed brachiation, primates like gibbons adopt a different mechanism of swinging that has a non-contact flight phase that minimizes branch contact collision energy loss. The critical factor in successful high-speed brachiation is coordination of the end of the flight phase and the beginning of contact phase (Bertram & Chang, 2001). This point minimizes a mechanical collision and the loss of energy between the animal and the support surface at contact (Bertram & Chang, 2001). Energy loss is minimized at contact due to the path of the subject's center of mass at the end of the flight phase being tangential to the path of the center of mass at the end of the arm at the beginning of support phase (Bertram et al., 1999). This mechanism reduces energy loss and is unlike human running, as there is no elastic storage and recovery process (Usherwood et al., 2003).

High variability has been observed in swing kinematics of primates (Bertram et al., 1999; Usherwood et al., 2003). Primates have shown remarkable adaptability in brachiation, particularly at high velocities, that are difficult to replicate in terrestrial gait. Locomoting through complex forest canopies requires adaptation to changes in branch placement and strength, as well as conditional changes to weather and carrying objects (Usherwood et al., 2003). The forearm kinematics and support/ground reaction forces of primates brachiating tend to be less directionally predictable than the lower extremity during quadruped walking (Demes & Carlson, 2009). Brachiating introduces more variable limb support environment and balance demands. The biomechanical consequences of this are greater support reaction force and limb excursion angle variability than terrestrial locomotion (Demes & Carlson, 2009). Changes in the oscillation frequency of swing is mostly determined by the distribution of body mass in the swinging animal, and the acceleration due to gravity which is constant (Bertram & Chang, 2001). The ability to change each step to the environmental demands is a behavior demonstrated in brachiation, and rarely in terrestrial gait (Bertram et al., 1999). High variability in the mechanics of the upper limb is in line with the need of a more mobile and less stable upper limb that has evolved for numerous non-locomotor functions (Demes & Carlson, 2009). Loading variability incorporates a great deal multi-axial forces on the bones of the limbs, creating bending forces. This may be a cause of the greater curvature in the shaft of long bones in arboreal animals such as chimpanzees (Demes & Carlson, 2009).

While brachiation accounts for the most active arboreal behavior, chimpanzees perform other important activities in arboreal settings, like hanging from trees. Axial rotation about the joints of upper extremity affords chimpanzees the ability to rotate their body 360 degrees in either direction during one arm hanging (Stern & Larson, 2001). This capability is important for chimpanzees, as they are able to feed in a hanging position, by using the free limb for grasping food efficiently (Stern & Larson, 2001). This behavior requires full use of the rotational range of motion at the carpal joints and shoulder. When rotating about the one hanging arm, the forearm rotations through pronation and supination only account for approximately 180 degrees of body rotation (Stern & Larson, 2001). The other 180 degrees of rotation is provided mostly through the glenohumeral joint and somewhat through the midcarpal joints (Stern & Larson, 2001).

2.6.3.1 Primate Shoulder Muscular Activity during Brachiation

The role of the shoulder muscles during brachiation has some similarities between primates. Differences in muscle size, attachment site and size, and use are typically associated with differences in terrestrial and arboreal locomotor strategies – humans being habitual bipeds, chimpanzees both terrestrial and arboreal, orangutans being mostly arboreal (Larson & Stern, 2013; Stern & Larson, 2001). Approximately 60-70% of an animal's body mass is attributed to locomotor usage (Grand, 1977). The distribution of the mass differs between animals and is dependent on the specific locomotor behaviors (Thorpe et al., 1999). The upper limb of humans accounts for approximately 9% of body mass in humans, and 16% in chimpanzees (Zihlman, 1992). Dissections of the musculature of human and chimpanzee upper extremities reveal that chimpanzees have larger muscle masses, fascicle lengths and physiological cross sectional areas than humans (Bertram & Chang, 2001; Thorpe et al., 1999).

The shoulder musculature has an important role in the control of brachiation trajectory, as well as stabilization of the glenohumeral joint in chimpanzee (Bertram & Chang, 2001). The use of the upper extremity for locomotive purposes in chimpanzees requires that the joints be able to produce greater joint moments. Terrestrial quadrupedalism accounts for the majority of chimpanzee locomotion, but brachiation accounts for the most strenuous activity in which chimpanzees engage (Thorpe et al., 1999). Brachiation is more strenuous due to the effects of gravity on the musculoskeletal system, and its bimanual, discontinuous and three-dimensional nature (Thorpe et al., 1999). This greater locomotor demand of the upper extremity in chimpanzees is met with greater relative muscular force capability and an upper extremity that accounts for a greater percentage of total body mass than in humans (Thorpe et al., 1999; Zihlman, 1992). The greater absolute PCSA allows muscles to exert greater forces due to a higher number of sarcomeres (Zajac, 1992). The greater fascicle length indicates the number sarcomeres in series and increases the maximum shortening velocity of a muscle (Zajac, 1992). Electromyographical (EMG) data available on primates, though limited by the number of muscles and subjects observed, provides insight into the muscular control of the upper extremity.

The trunk musculature, particularly that which connects the trunk to the arm, is active during arm elevation, and assists in accelerating and decelerating the subject to prepare for flight phase and oncoming support contact in an effort to avoid collision (Bertram & Chang, 2001). More developed trapezius and serratus anterior are noted in primate species that use overhead shoulder postures to climb, such as monkeys and chimpanzees (Oxnard, 1969). The boney insertion sites for both these muscles are also enlarged in these species, which can provide greater leverage (Takahashi, 1990; Taylor, 1997). The serratus anterior and trapezius muscles upwardly rotate the scapula in non-human primates, allowing upward rotation of the glenohumeral joint in arm elevation (Green, 2013). These adaptations to the trunk musculature provide mechanical advantages in brachiating primates that have possibly evolved out of modern humans, as these same muscles are scapular retractors in humans (Oxnard, 1969).

Subscapularis is primarily an internal rotator of the arm in primates (Larson, 1988). This muscle’s activation is strongly associated with hand orientation and is usually inactive during quiet overhead suspension (Larson, 1988). The contribution of this muscle to upper extremity behaviors has been examined between primates with similar brachiating behaviors such as chimpanzees, orangutans, and gibbons (Larson, 1988; Larson & Stern, 2013). During overhead swing, subscapularis aids in the internal rotation of the arm through swing from its initial orientation in extreme external rotation (Larson, 1988). Subscapularis is also active in raising the arm in the mid to latter half of swing to control internal rotation and stabilize the glenohumeral joint (Larson, 1988). The subscapularis is not as active during support in chimpanzees as in other more arboreal primates like gibbons (Larson, 1988). Gibbons have low humeral torsion, which repositions the elbow in more external rotation. This morphological adaptation is a result of primarily locomotor behaviors that often require extreme elbow axial rotations, optimizing the upper extremity for arboreal behaviors (Larson, 1988). The greater humeral torsion in chimpanzees, and consequently lower activation of the subscapularis muscle is posited to be the result of a compromise between arboreal and quadrupedal terrestrial behaviors (Larson, 1988).

Infraspinatus and supraspinatus are integral to overhead arm elevation activities in brachiating primates (Larson & Stern, 2013). Infraspinatus is much larger than supraspinatus in chimpanzees, and has one of the largest relative sizes of all primates (Larson & Stern, 2013). Infraspinatus is the rotator cuff muscle that is most active in glenohumeral joint stabilization in chimpanzees during support phase of brachiating swing (Larson, 1988; Larson & Stern, 1986). Infraspinatus, along with supraspinatus, has high activity during the elevation phase of the second half of swing in brachiation (Larson & Stern, 2013). It is believed that supraspinatus and infraspinatus aid the deltoid by abducting the arm. Supraspinatus appears to be the primary aid to the deltoid in abducting the arm, and may also help resist the superior displacement of the humerus caused by activation of the deltoid (Larson & Stern, 2013). In the second phase of swing, the infraspinatus becomes more active as elevation of the body occurs (Larson & Stern, 2013). These observations have been detected in chimpanzees, orangutans and gibbons (Larson & Stern, 2013).

2.7 Morphological Contrasts Between Primate Species

Anthropologists and evolutionary biologists have contrasted the musculoskeletal morphology of chimpanzees and humans, including the upper extremity, to better understand what features distinguish the species in their physical capabilities. Chimpanzees have much greater variety of locomotor behaviors than modern humans. As a terrestrial and arboreal locomotor animal, the chimpanzee upper extremity represents a compromise between multiple locomotor forms. On the other end of the spectrum, the human upper extremity represents a non-weight-bearing, non-locomotor extremity. Musculoskeletal morphological changes to the shoulder have meant differences in locomotor behaviors between humans and chimpanzees. However, both species share what is hypothesized to be a common arboreal ancestor. How each evolved to their present form, and how humans potentially devolved their arboreal capabilities in their upper extremity is unknown. Analyzing the differences in upper extremity morphology between the two species, as well as other great apes, has been used to understand the evolution of human upper extremity capacity and inform analyses of ancient human remains. Identification of what musculoskeletal features are associated with specific species and physical abilities guides conclusions about the upper extremity functional capacity of ancient and modern humans.

2.7.1 Morphological Comparisons in Anthropology

Most fossil and extant animal comparative morphological analyses have focused largely on the skull - cranial, mandibular and dental morphology (Zihlman et al., 2008). Skulls are typically more numerous, and make a more abundant source of data. The greatest depth of morphological data on chimpanzees is in cranial data (Uchida, 1996). This includes craniometrics, mandibular morphology, and dental metrics and morphology. Dental and cranial features have been assumed to be more representative of within species phylogeny as they are least subjected to homoplasy (Larson, 1998). However, this is in contradiction to the fact that most functional and comparative studies are on other parts of the anatomy (Zihlman et al., 2008; Uchida, 1996). Though less reliable for phylogenetic study, postcranial features are considered to be more representative of function than phylogeny (Larson, 1998).

Using postcranial morphological traits to assess taxonomic groups, phylogeny and functional associations is sensitive to the traits used in the analysis (Young, 2005). It has long been assumed that the postcranium contains more functional data than phylogenetic (Young, 2008). Therefore, when making postcranial analyses between species, a strong reasoning for choice of morphological traits must be made, as postcranial features are more influenced by function than cranial features (Young, 2005). Depending on the form of morphological analysis, results are often only weakly correlated with molecular estimations of phylogeny. Increasing the number of traits and landmarks included in the assessment does not necessarily increase the strength of the correlation, but can actually confound the analysis further (Young, 2005). Post-cranial features must be chosen for their functional importance with concurrent consideration of their association with phylogeny. This increases the usage of post-cranial morphology is assessing and correlating species phylogeny and locomotor behavior (Young, 2005). It can also broaden the type of data used to make phylogenetic analyses beyond cranial data, which doesn't take into account the influence of function and locomotor behavior on species distinction (Young, 2005). The scapula is of particular interest as it is one part of the three joints at the shoulder – the acromioclavicular, sternoclavicular and glenohumeral joints – and is the attachment site for numerous upper limb, back and neck muscles (Young, 2008). An example of such a morphological analysis on the scapular feature of glenoid inclination is present in Figure 9. Quantifying these biological features, including within- and between-species variation, ensure a metric for identifying and naming species. It also provides a means for placing features of interest appropriately on a spectrum of ape-like to human-like based on morphology (Uchida, 1996; Young et al., 2015).

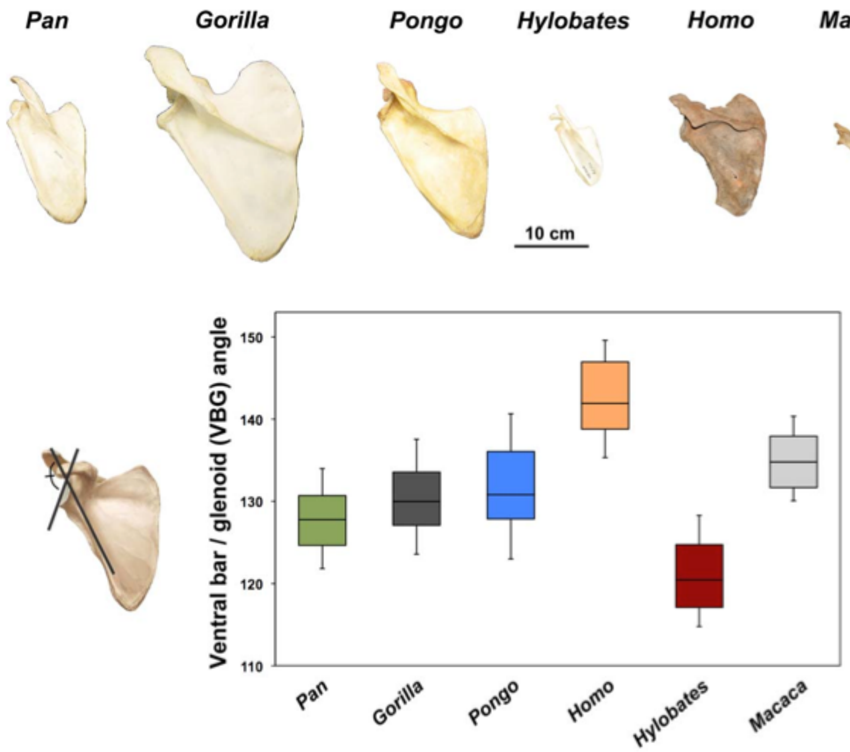


Figure 9: Example of how a boney morphological feature can be used to differentiate between related species of primates. (Green, 2013). The four great apes species are analyzed, along with more distantly related primate species of *Hylobates* and *Macaca*. The bar-glenoid angle gives an indication of the orientation of the glenoid with respect to the position of the scapular body. Humans (*Homo*) differ from all other primate species in this trait, including their closest relatives of chimpanzees (*Pan*), gorillas (*Gorilla*) and orangutans (*Pongo*).

2.7.2 Morphological Study of the Upper Extremity

Morphological variability of the modern human and chimpanzee upper extremity bones as it relates to shoulder function has been extensively documented. In humans, much of this work has been conducted to improve reconstructive arthroplasty and other surgical procedures (Bueno et al., 2012). These studies often aim to correlate the shape and size of the reconstructed portion of pathologically damaged or fractured bone with the remaining healthy portions of bone (Bryce et al., 2008; Bueno et al., 2012; Kwon et al., 2005; Pearl, 2005). Malalignment or disproportional shape and size of reconstructed bone can lead to abnormal loading, and failure of the surgical procedure (Bryce et al., 2008; Pearl, 2005). With regards to chimpanzees, these studies are often conducted through anthropological research.

The aim is to compare morphological form between extant ape species with fossil bones of ancient and extinct hominoid species. Relationships are drawn between specific boney features and locomotor differences in living apes (Larson, 1998; Young, 2005). Certain bone features have been correlated with arboreal or terrestrial behaviors. This process is an attempt to gain retroactive insight into locomotor abilities of ancient hominoids and the evolution of the human species by comparing bone traits in fossilized remains to functionally correlated bone features in apes. Despite different reasons for analyzing morphology in each species scenario, similar bone features are often assessed. As more data is been collected for each species, the association with locomotion and ranges for the variability of these morphological traits have been begun to take form.

A number of morphological features of the scapula have received attention by being associated with specific hominoid species and locomotive behaviors, particularly in distinguishing between arboreal and terrestrial behavior (Taylor, 1997). Commonly analyzed anatomical features include scapular body shape, glenoid shape, glenoid inclination, length and width of the acromion, and length of the coracoid process (Bryce et al., 2008; Bueno et a., 2012; Churchill et al., 2001; Kwon et al., 2005; Ohl et al., 2013; Welsch et al., 2003). Some scapular features have been identified as characteristic of the 'ancestral hominoid morphotype'. These include a more posteriorly positioned scapula, a superior-inferiorly elongated scapula, long acromion and coracoid processes, a deepened spinoglenoid notch, and a widened glenoid fossa (Figure 10) (Larson, 1998). Many of these features are thought to bear anthropological significance, as they have a myriad of effects on the function of the shoulder (Carretero et al., 1997; Churchill et al., 2001, Haile-Selassie et al., 2010; Larson, 2012). But the degree to which they affect function, if at all, is not fully understood,

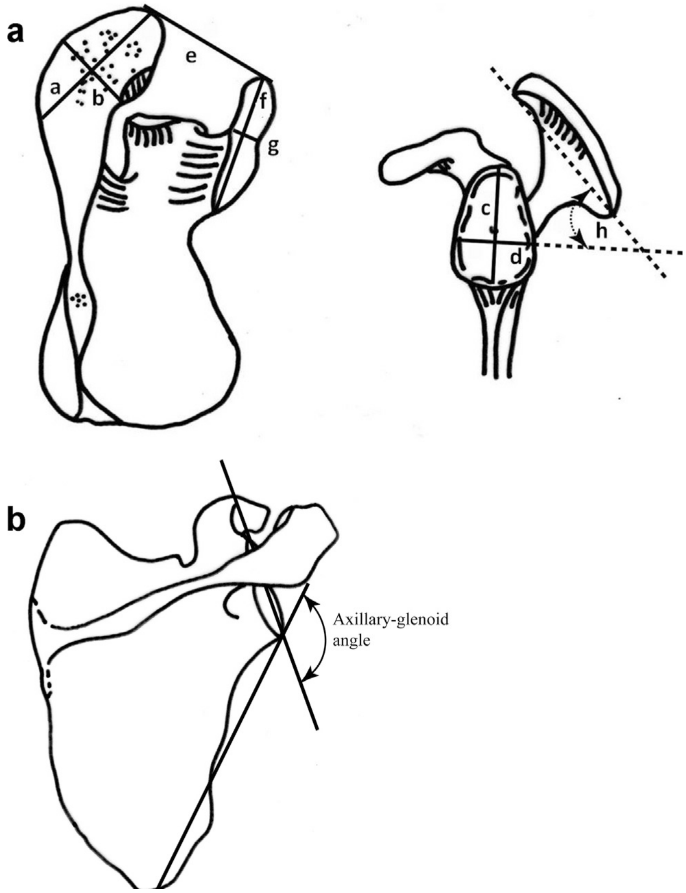


Figure 10: Example of some measurements of the scapula. a: greatest length measured along the long axis of the acromion; b: width of the acromion; c: height of the glenoid cavity; d: width of the glenoid cavity measured; e: distance between the tips of the acromion and coracoid process; f: length of the coracoid process; g: width of the coracoid process; h: slope oft he acromion; i: axillary-glenoid angle, indicating glenoid inclination (Voisin et al., 2014).

Some inferences have been made regarding the association of scapular morphology with shoulder function. The shape of the acromion and corocoid process greatly affect the function of the shoulder. The shape and orientation of the acromion process changes the subacromial space, through which the supraspinatus muscle, long head of the biceps tendon and the subacromial bursa pass (Lewis et al., 2001; Voisin et al., 2014). Decreases in the size of this space impinge these tendons, leading to tendon tears and rotator cuff pathology (Lewis et al., 2001). Scapular body and spine shape affect the size and orientation of muscle attachment sites, altering effective muscle contribution the range of motion the shoulder joints (Green, 2013; Inman et al., 1944). The orientation and shape of the glenoid affects glenohumeral range of motion (Kwon et al., 2005; Roach et al., 2014).

Analogous work has been done assessing the morphology and variability of the humerus and clavicle. Like the scapula, these studies mostly focus on either the association of a bone trait with locomotor function or improving surgical outcomes in bone reconstruction and reshaping (Hromadka et al., 2006; Larson, 1998; Pearl, 2005; Robertson et al., 2000; Taylor, 1997). The proximal humerus is of particular interest as its articulations with the glenoid affect function of the glenohumeral joint (Carretero et al., 1997; Hromadka et a., 2006; Pearl, 2005; Robertson et al., 2000). Additionally, numerous muscles attach to the greater and lesser tubercles of the proximal humerus, making the size and orientation of these features integral to muscle function at the shoulder. The proximal humerus is highly variable, both between humans, and even between left and right arms (Boileau & Walch, 1997; Pearl, 2005). In honinoids, the humeral head is larger and rounder, keeping with the enlarged glenoid fossa also found in the great apes. Great apes also have lower deltoid insertion, deep and well-defined olecranon fossa with a lateral trochlear keel that wraps around distally to meet the olecranon, and modified curve of the humeral shaft (Larson, 1998). These features affect the moment arms and leverage of the arm and shoulder musculature. Humeral torsion – the angle created between the articulating surface of the humeral head and an axis that crosses through the epicondyles – is also an important trait that affects axial rotation of the arm, being associated with capacity for overhead throwing (Roach et al., 2013; Robertson et al., 2000). Lower humeral torsion in humans increases the range of external rotation of the glenohumeral joint, improving throwing projection speed (Roach et al., 2013).

As a small bone, only a few morphological features have been assessed in the clavicle. There is also less data on the morphology and form-function relationship in the clavicle (Auerbach & Raxter, 2008). However, as one half of both the acromioclavicular and sternoclavicular joints, the clavicle is an essential strut connecting the shoulder to the axial skeleton and transmitting load between the arm and thorax (Auerbach & Raxter, 2008; Daruwalla et al., 2010; Fatah et al., 2012;

Pronk, 1991). The clavicle is also the attachment site for a number of important upper extremity muscles and ligaments. The force transmission from activation of these muscles is the likely cause of the clavicle's S-shaped curvature (Auerbach & Raxter, 2008). The effect of this role in joint function and load bearing creates high levels of variability in the bone that somewhat mimics that seen in the humerus (Auerback & Raxter, 2008). The clavicle's depth, length and curvature is of great importance to the overall function of the upper extremity. Clavicular features that have drawn interest for affecting the role of the clavicle in joint function include maximum length, medial (sternal) and lateral epiphysis maximum and minimum diameter, conoid diameter, conoid-acromion distance, and axial twist angle (Carretero et al., 1997; Daruwalla et al, 2010; Fatah et al., 2012)

2.7.2.1 Anthropologically Significant Morphological Traits

While a number of traits have been identified as characteristic of humans and their primate relatives, the interplay between these traits, and the specific contribution and role of each in functional capacity is uncertain. Morphological features of the shoulder that are considered anthropologically significant are included in Table 1. The specific significance of these features varies. Those such as humeral torsion and the glenoid orientation have been associated with capacity for throwing and overhead capacity, respectively (Larson, 1995; Roach et al., 2013). However, others appear to be morphologically characteristic to a species or taxa, with little understanding at present of the trait's functional role. But the uniqueness of these features within certain primate species make them evolutionarily significant and potentially relevant to human shoulder function. These common hominoid features might be inherited from the last common ancestor, and would possibly be indicative of the locomotor form of the common ancestor and be the root of specific capacities and limitations of the modern human shoulder (Harrison, 1987; Larson, 1998).

Table 1: Anthropologically and functionally significant morphological traits in the hominoid shoulder, and their hypothesized relation to species function and physical ability.

Feature	**Functional Significance**
Scapular body shape	Width-to-height ratio is associated with rotator cuff muscle origins and line of action (Larson, 1998)
Scapular Spine Orientation	Increased angle associated with increased capacity for arm elevation through action of trapezius and serratus anterior that upwardly rotates the scapula (Ashton & Oxnard, 1964)
Glenoid Orientation	More cranial orientation of glenoid in arboreal animals (Larson, 1998)
Glenoid Shape	Wide glenoid found in arboreal primates (Larson, 1998; Young, 2006), with cranial elongation in great apes (Young, 2003).
Subscapular Fossa	Fossa expands laterally in brachiators as it is active in pull-up phase of vertical climbing (Larson, 1995)
Deltoid insertion	Primary arm abductor, necessary for brachating behaviors (Larson, 1995)
Infraspinatus insertion orientation	Muscle is thought to be primary synergist to deltoid in arm abduction through superolateral orientation of its insertion on greater tubercle in brachiators (Larson & Stern, 1986)
Subscapularis insertion orientation	Change in orientation creates greater differentiation between proximal and distal muscle fibers, indicating greater shoulder mobility (Larson, 1995).
Relative acromion length	Projection of the acromion affects the size of the subacromial space and risk of impingement (Larson, 1995; Larson, 1998; Lewis et al., 2001)
Relative Shoulder Breadth	Distinguishes hominoids from other primates. Related to thoracic shape (Larson, 1998)
Relative Sternal breadth	Distinguishes hominoids from other primates (Larson, 1998).
Humeral Head shape	Rounded shape of the humerus has been associated with more committed arboreal primates (Larson, 1998)
Bicipital groove width	Insertion site for biceps tendon, active in brachiation and arm rotations during one-arm hanging (Larson & Stern, 2001)
Humeral Torsion	Lower torsion increases range of external rotation about the shoulder, affecting overhead throwing speed (Roach et al., 2013).

Some of these morphological features have been identified as being characteristic of the hominoid family or the chimpanzee species. While functional significance is not always firmly attached to these specific traits, they may have importance to the species-specific functional capacity that has yet to be explored. Multivariate analyses of primate upper extremity features, using these traits of the clavicle, humerus, scapula and thorax have shown that the hominoid shoulder is distinct from other primates (Young, 2003). Within hominoids, chimpanzees and gorillas have the most morphologically similar upper extremity (Young, 2003). Specific to the scapula, the features that best distinguish between species of great apes (chimpanzees, bonobos, gorillas, and orangutans) are length and angle of the scapular spine, shape of the glenoid, and geometry of the scapular blade (Young, 2008). These traits are distinctive between species at birth and remain fairly unaltered through development (Young, 2008). Despite being distinctly hominoid, these features also demonstrated high variability. If and how these hominin features and their variability relate to modern human function is not fully understood.

2.7.3 Variability in Shoulder Morphology

Upper extremity morphology varies between primates as a result of differing functional and locomotor behaviors (Alemseged et al., 2006; Young, 2006). The postcranium of the chimpanzee demonstrates morphological compromises between arboreal and terrestrial behaviors (Pontzer & Wrangham, 2004). Recent studies have demonstrated that there is phylogenetic structure in the postcranium of mammals (Young, 2003). There has been some work quantifying the shape and variability in features of the primate shoulder bones, to distinguish between species and relate bone form to locomotor activities (Larson, 1998; Young, 2003, 2005, 2008).

Locomotor behaviors affect bone shape in the upper extremity (Carlson, 2005; Young, 2006). Those that involve changes in direction of movement may cause adaptive changes to bone shape in multiple directions as an adaptation to the mechanical environment (Carlson, 2005). Thus, there may be more variability in the bone shape of arboreal animals. Bending is the primary deformation force that bones experience during locomotion (Biewener, 1983; Carlson, 2005). Work by Demes and colleagues (2009) demonstrated that primate arboreal locomotion tends to cause more multi-directional bending loads than terrestrial locomotion. Arboreal locomotion must be adapted to the variable size, shape and positioning of support branches, while the ground typically provides a predictable and less variable support surface for terrestrial locomotion (Carlson, 2005). This causes limb position and subsequent bending forces to vary widely in arboreal conditions experienced by some primates such as chimpanzees. The result is likely greater within-species morphological variability in those that conduct arboreal locomotion.

Greater variability of locomotor behaviors also increases variability of the features of the upper extremity (Young, 2006). The scapulae of primates that engage in non-quadrupedal behaviors, such as chimpanzees, gorillas, orangutans, and bonobos, are more variable than primates that are committed quadrupeds (Young, 2006). Committed quadrupedal primates show greater morphological similarity within species (Young, 2006). The scapula of primates who are not committed quadrupeds is less specialized due to upper extremity involvement in both terrestrial and arboreal behaviors (Young, 2006). This strengthens the inference that the shape and form of the bones of the upper extremity are sensitive to the type(s) of behaviors to which they are exposed. Between-species morphological variability is greater among primates that partake in a greater diversity of locomotor behaviors. Further, within-species variation is greater in those primate species that exhibit greater variability in locomotor behaviors (Young, 2006).

Variability of morphological features is important to study due to the effect it can have on the range of possible physical abilities in individual species. The level of morphological variability for each primate species is species-specific, due to species-specific behavior (Young, 2006). There is ambiguity regarding aspects of the evolutionary biology of the great apes, particularly chimpanzees, who are of most interest to human biology and evolution. Humans and chimpanzees are genetically and biologically distinct species. To begin to understand any relationship between shoulder form and function in chimpanzees and humans and how it dictates modern human function, the differences between species in morphological traits of the shoulder bones and shoulder physical capability need to be quantified. Robust assessment of the hominin fossil record requires extracting as much morphological information about the natural variability in living hominins as possible (Guy et al., 2003). This means defining the range of intra-species variation in both modern humans and chimpanzees, and the degree of morphological distinction in skeletal traits of the shoulder between each species. Thus work is needed distinguishing between the modern human and chimpanzee shoulder from a morphological and functional standpoint.

2.8 Limitations to Current Anthropological Assessments of Morphology

Locomotor information on archaic hominin fossilized species is largely heuristic, and could benefit from dedicated quantitative analyses. The fossil record leaves scarce clues as to the course of human evolution to the current form. Bones are all that remain, no nerves, muscles or other soft tissues. Even the original environmental landscapes on which these ancient ancestors lived are lost, and must be recreated through evidence buried in the geological record. The only primary information available to physical anthropologist regarding extinct hominoid species is structural bone information contained in fossils. Anthropologists typically use measurement of bone morphology to identify structural evolutionary changes and infer functional adaptations (Hutchinson, 2012; Lauder, 1995; Oxnard, 1969). This method allows structural form to inform the understanding of function in an organism using what remains of extinct species (Lauder, 1995; Wang, 2004). The anthropological literature has been dominated by comparative analyses of morphological traits.

This method of morphological comparison can enable general predictions of species function, but is problematic for precise inferences regarding function from morphology (Lauder, 1995). Comparative methods can lead to inconclusive evidence regarding the pathway that led to the modern human shoulder. The uniqueness of human habitual bipedalism leaves traditional anthropological methods of analogizing to reconstruct locomotor behavior incomplete, as humans remain the only living example from which to make comparisons (Wang et al., 2004). This uniqueness has made reconstruction of extinct hominin behavior and inferences regarding the pathway toward modern human behavior difficult through comparative morphological analyses.

Much of human evolutionary morphology comparisons have focused on implications and importance of ape-like features versus human-like features (McHenry, 1994). Correlation between boney articulations of modern humans and extant apes that are close living relatives, as well as extinct hominins can be made to infer the evolutionary pathway that created the modern human form (Oxnard, 1969). Relating morphological form to functional capacity is dependent on the specific analysis used, and only considers specific features, and not the musculoskeletal system as a whole. Many anthropological inferences are based solely on singular structural comparisons between fossil specimens, or grouping a few select architectural features. These methods may have led to erroneous conclusions about the evolution of the human shoulder, as function and structure are not tightly correlated (Lauder, 1995; Oxnard, 1969).

Comparative morphological analyses are problematic for a number of reasons. They tend to only yield global conclusions regarding a particular joint's function (Pronk, 1991). When trying to infer overall joint function from specific, singular anatomical features, the effect and contribution of each feature to joint function is not necessarily equal (Oxnard, 1969) and cannot be accurately and confidently quantified. Multivariate analyses of these architectural measures lead to more confusion. Deciding which features to include can produce vastly different conclusions. Correlations can be made between structures and function, but the degree of correlation is related to the statistical methods and hierarchy used (Churchill et al., 2013; Oxnard, 1969).

Many physiological, neurological, biomechanical and environmental factors interact to define the function and capability of an organism. Inferring physical ability from boney morphological traits alone is likely simplistic and misrepresents function (Hutchinson, 2012; Lauder, 1995). Though worth analyzing to quantify its role, bone morphology is just one component of the greater complexity that defines physicality ability. A true understanding of joint function, and the effect of bone morphology on it, must integrate all parts of the biological system that creates movement. Computational musculoskeletal modeling can offer a method of assessing the contributions of varying musculoskeletal adaptations through modeling of behaviors and testing the sensitivity of certain musculoskeletal features on joint function (Hutchinson, 2012).

2.9 Biomechanical Modeling in Anthropology

Using only structural properties of fossils to inform hypotheses regarding the evolution of musculoskeletal function is limiting, especially in extinct species and taxa for which the hypotheses cannot be proven (Hutchinson, 2012; Lauder, 1995). For ancient human ancestors, limited data found in fossilized bones is all that is available to researchers to infer functional capabilities. Knowledge of muscular, neural, behavioral and even environmental factors is necessarily reduced to informed assumptions. These missing pieces of information factor in to how structure informs function, as all these factors interact to inform the physical capabilities of an organism (Hutchinson, 2012).

Computational biomechanical models simulate functionality by incorporating properties of musculoskeletal function and motor control dynamics using information obtained from musculoskeletal structure (Hutchinson, 2012). A biomechanical model includes the complex interaction between boney structure and all other physiological factors being modeled, as well as the specifics of muscle physiology and segment properties. Further, each linked-segment interacts with all others to affect muscle function and physical capabilities (Hutchinson, 2012; Zajac et al., 2002). This allows for more guided and quantitative inferences regarding what the organism is physically capable of performing.

Biomechanical modeling is not without its complexities, assumptions and hurdles. Modeling approaches advance as computational capacities and knowledge of the musculoskeletal system improve. Researchers are still discovering the complexities of the human body. At present, most computational models cannot reflect true human ability without assumptions about musculoskeletal properties and limits, imposed musculoskeletal boundaries, and external checks with experimental data. There is always a trade off between model reductionism and realism (Hutchinson, 2012). Validation procedures allow tacit quantification of just how much a model represents reality (Hutchinson, 2012). Issues such as these are exasperated when modeling non-human animals and extinct organisms for evolutionary purposes. Biological data becomes less available, requiring new compromises to be made based on the data of close relatives and theoretical assumptions.

2.9.1 Biomechanical Modeling of the Shoulder

Despite being a site of intriguing complexities, and occupational and recreational injuries and disorders, computational modeling of the human shoulder is still in the beginning stages compared to work done on other segments of the body (Rau et al., 2000). Study of this region of the body in humans and other animals can give insight to the unique functionality of the human upper extremity for daily activities like reaching, grasping, gesturing and typing, to athletic feats such as swimming and throwing (Rau et al., 2000). To study the shoulder, computational biomechanical modeling requires understanding of shoulder mechanics that drive a musculoskeletal model.

2.9.2 Shoulder Mechanics

Movements at the shoulder in humans are much more variable than those of the lower extremity (Rau et al., 2000). The lower extremity is primary used in locomotor activities, and follows cyclical patterns of symmetrical movement (Rau et al., 2000). In committed quadrupedal primates, the lower and upper extremities maintain cyclical movements (Pontzer et al., 2014). However, the human and chimpanzee upper extremity is used in a more versatile and broad manner, with greater bilateral differences in humans. Motions at the shoulder occur through three-dimensional rotational contributions and cannot be simplified to two-dimensional rotations (Rau et al., 2000). The large range of three-dimensional motions at the shoulder, and gliding motion of the scapula under the skin introduces greater soft tissue artifact that requires new and continually improving procedural approaches to obtain accurate biomechanical data.

The large range of motion at the shoulder is provided through the interaction of three joints that compromise the shoulder – the glenohumeral joint, acromioclavicular and sternoclavicular joint (Teece et al., 2008). Most of the motion of the shoulder takes place at the glenohumeral joint (van der Helm & Pronk, 1995). Additional motions occur due to the three-dimensional rotations of the scapula and clavicle. The sternoclavicular and acromioclavicular joints combine to create scapulothoracic motion (Inman et al., 1944). These joints create interactions between the clavicle and thorax, and scapula and clavicle, respectively. Rotations of the scapula and clavicle bones in elevation, rotation, and retraction provide additional range of motion at the shoulder (Teece et al., 2007; Veeger & van der Helm, 2007). External rotation of the scapula is particularly important, as it allows greater elevation of the arm (Magermans et al., 2005).

The glenoid provides modest intrinsic stability to the glenohumeral joint. In humans the glenoid is shallow. The lack of depth in the fossa allows the humeral head great mobility, and concomitantly high risk for dislocation. Stability in the glenohumeral joint is instead provided through several other mechanisms – muscle activation, ligament tension, labrum deformation, joint suction, adhesion and cohesion, articular version, proprioception and negative internal joint pressure (Cole et al., 2007; Schiffern et al., 2002). The interaction of these mechanisms to provide both stability and mobility necessary for shoulder function is complex. Biomechanical techniques to model the shoulder need to incorporate the contributions of all these mechanisms to reflect physiological shoulder stability (Dickerson, 2008).

Motion and stability at the shoulder depends on integrated mechanisms. Ligaments behave as checkreins at the shoulder (Lugo et al., 2008). They are lax in mid-range postures, but become taut at end-range (Veeger & van der Helm, 2007). This maintains mobility while preventing end-range joint dislocation. The glenoid labrum – a fibrous ring around the periphery of the glenoid – increases the depth of the glenoid by approximately 50% (Figure 11) (Howell & Galinat, 1989). The stability provided by the labrum depends on its deformation as the humeral head rotates in the glenoid, joint compressive force magnitudes, and articular integrity (Veeger & van der Helm, 2007). Joint suction occurs when compressive forces into the glenohumeral joint create a suction force into the glenoid and labrum (Matsen et al., 1994). Joint cartilage fluid forces also create adhesion and cohesion in the glenoid fossa by acting as a sealant, enhancing the effect of suction (Matsen et al., 1994). Articular version is the anatomical orientation of bones that make up this region. The scapula is typically oriented at approximately 30° internal rotation, 3° protraction and 20° anterior tilt (Lugo et al., 2008). This provides a boney shelf to maintain and stabilize the humerus in the glenoid, particularly in opposition to gravitational forces. Proprioception provides sensory feedback to the joint regarding position and movement control. Though still not well understood in the shoulder, it is likely provided through ligamentous stretch sensors and only active near end ranges of motion (Veeger & van der Helm, 2007). Lastly, a negative intra-articular pressure in the glenohumeral joint creates resistance to pulling forces (Gibb et al., 1991), providing a small amount of stability to the joint by limiting translation of the humeral head (Veeger & van der Helm, 2007). Complimentary to all these mechanisms are compressive, stabilizing forces provided by muscular actions.

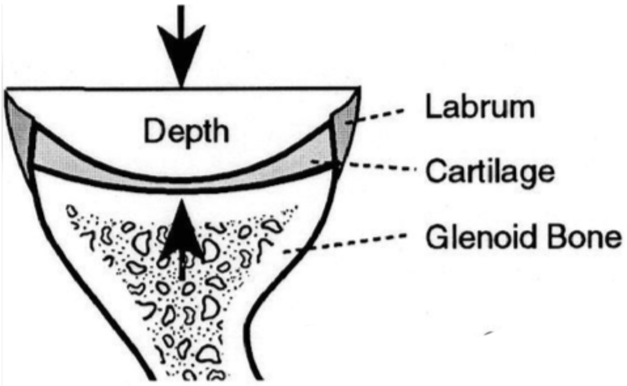


Figure 11: The labrum adds depth to the glenoid fossa, increasing stability. Deformation of the glenoid increases conformity between the translating and rotating humeral head and the glenoid fossa, also increasing glenohumeral stability (Matsen et al., 1994).

A great many number of muscles contribute to motion and stability at the shoulder (Dickerson, 2008). The majority of joint stability is provided by active muscular contraction that directs the net joint reaction force into the glenoid (Figure 12) (Veeger & van der Helm, 2007). Seventeen muscles originate or insert onto the human scapula, all of which guide and stabilize scapulothoracic motion (Lugo et al., 2008). These muscles, such as the trapezius, levator scapulae, rhomboids, serratus anterior, pectoralis minor and subclavius, control articulations that occur in the space between the posterior thorax and anterior scapula (Terry & Chopp, 2000). Large muscles like latissimus dorsi, serratus anterior, pectoralis major and the deltoid create large joint moments about the shoulder. Activation of these muscles creates greater compression at the shoulder and subsequent joint stability (Lugo et al., 2008).

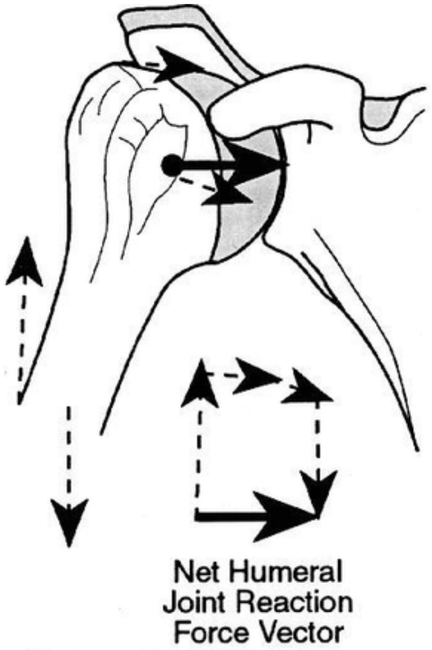


Figure 12: The contraction of the muscles around the shoulder (shown as the dashed arrows) collectively work to direct the net joint reaction force of the glenohumeral joint (shown as the solid arrow) into the glenoid (Matsen et al., 1994).

The rotator cuff muscles all have individual bony motion actions but together contribute to overall glenohumeral stability (Lugo et al., 2008). The rotator cuff consists of the supraspinatus, infraspinatus, teres minor and subscapularis muscles (Figure 13). These muscles are located very close to the glenohumeral joint center and have small moment arms. Unlike the larger muscles that create large joint moments in humans, the rotator cuff muscles provide fine control of translational and rotational motions. Activation of the rotator cuff muscles creates controlled compression into the glenoid, decreasing shear forces and stabilizing the joint (Veeger & van der Helm, 2007). This helps to center and stabilize the humeral head into the glenoid (Lugo et al., 2008).

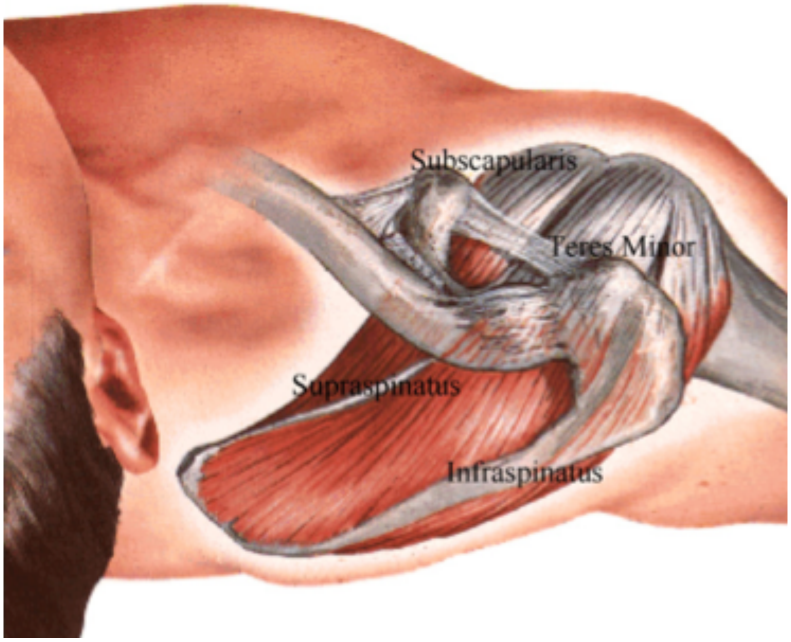


Figure 13: Transverse view of the four rotator cuff muscles of the shoulder (from Lugo et al., 2008).

Traditional biomechanical models have taken an inverse dynamics approach, using experimental kinematic and kinetic data to determine external joint forces and moments. While useful, this data is limited and provides little information on the muscle forces, internal joint forces or the contribution of stability mechanisms to complex regions such as the shoulder. Computational biomechanical approaches provide the opportunity to model all the components of a body region that contribute to its movement. This includes bone shape, muscles, ligaments and other soft tissues and how they all interact to assist and restrict movement. This is especially useful at the shoulder, were there are multiple joints and contributors to stability. There are three parts to creating a model of the shoulder: geometric reconstruction of the region, calculation of external forces and moments, and a mathematical solution for solving the force load-sharing between soft tissues that also provides appropriate joint stability (Dickerson, 2008).

2.9.3 Geometric Reconstructions

Building a musculoskeletal model of the shoulder requires access to information on the geometry and architecture of bone and soft tissues. This data is integral to subsequent parts of a biomechanical model, as they are necessary to determine how muscles share force loading. The most useful source of this information for humans and chimpanzees has been from cadavers (Dickerson, 2008; Walker, 2009). In vivo medical imaging methods have also been attempted, however there is difficulty obtaining information on all components of the shoulder (Juul-Kristensen et al., 2000). Ultrasound, computed tomography and medical resonance imaging approaches often have a narrow scope of only a few muscles. From cadavers, bone shape and form can be determined, as well as locations of muscle and ligament origin and attachment sites (Garner & Pandy, 2001; Johnson et al., 1996; van der Helm et al., 1992; Veeger et al., 1991) The architecture, and mechanical properties and limits of these tissues as they contribute to joint stability have also been assessed through cadaveric experimentation in humans and chimpanzees (Debski et al., 1999; Johnson & Pandyan, 2005; Novotny et al., 2000; Pronk et al., 1993; Thorpe et al., 1999; van der Helm & Veenbaas, 1991; Walker, 2009; Zihlman, 1992).

Spatial data on tissues informs muscle line of action determination. Modeling muscle line of action requires knowledge of the muscle's path from cadaveric dissection. Using only a muscle's origin and insertion, the simplest mathematical models will design a line of action in a straight line connecting these attachment points. This is usually physiologically incorrect, as many muscles wrap around the bones that they articulate. Modeling techniques such as muscle wrapping have been developed to divert muscle paths around, instead of through, boney obstacles (Delp & Loan, 1995). Muscle wrapping modeling procedures produce more physiologically realistic results for muscle moment arms and forces (Gatti et al., 2007) than a simple attachment-to-attachment linear fit.

Bone orientation and kinematics are also integral to geometric construction of a shoulder model. Kinematics are particularly difficult to track in the shoulder, as the scapula and clavicle rotate and glide beneath the skin relatively more than other bones. The scapula rotates through three axes of internal/external rotation, anterior/posterior tilt and protraction/retraction, with the majority of scapular rotation occurring in internal/external rotation (Figure 14) (Ludewig et al., 2009). The three axes of clavicular rotation are elevation/depression, protraction/retraction and anterior/posterior rotation (Figure 15) (Ludewig et al., 2009). Traditional motion capture methods using skin-mounted markers cannot accurately measure the rotation of scapular and clavicular landmarks. This is problematic, as the closed-chain movement of the scapula and clavicle with arm movement is integral to understanding for the biomechanics of the shoulder (Veeger & van der Helm, 2007).

Scapular mobility is the main provider of the range of motion in the primate upper arm (Schmidt & Krause, 2011). In brachiating primates, large motions of the arm are highly reliant on large ranges of motion of the scapula (Jenkins et al., 1978). The opposite appears to be true during terrestrial quadrupedal locomotion, with the arm extending within a small range of motion without the aid of large or even moderate scapular rotations (Whitehead & Larson, 1994; Schmidt, 2005). Instead, the scapula provides stability to the shoulder during terrestrial locomotion. In humans, the scapula is not involved in any weight-bearing locomotor activities, as seen in arboreal locomotion of primate relatives. Instead, scapula motion provides the mobility of the shoulder necessary for non-locomotor tasks of daily living (Ludewig et al., 2009). In humans and closely related primates, the external rotation of the scapula provides the means for large excursions of the arm (Magermans et al., 2005; Schmidt & Krause, 2011)

Methods to mathematically predict the movement of the scapula and clavicle have been developed to overcome difficulties in experimentally tracking scapular and clavicular movements in humans. This approach assumes a predictable rhythm between the scapula and clavicle for given humeral movements (Inman et al., 1944). This closed-chain movement at the shoulder is deemed the shoulder rhythm, and predicts the previously defined three-dimensional rotations of the scapula and clavicle for a humeral movement (Inman et al., 1944). These equations can be used as part of the geometric reconstruction in a computational model to predict the movement of the scapula and clavicle from kinematic inputs of the humerus (Dickerson et al, 2007). The same scapular orientation is not always achieved with identical humeral motion, indicating that shoulder rhythm is highly variable

(Hogfors et al., 1991; Matsen et al., 1994). Scapular rhythm is also likely to be individual. Attempts have been made in humans to track shoulder rhythm with some degree of success (Ebaugh et al., 2005; Ludewig et al., 2004; McClure et al., 2001). These quantified rhythms have been represented mathematically as regression equations and used within musculoskeletal models (Dickerson et al., 2007; Grewal et al., 2013; Hogfors et al., 1991).

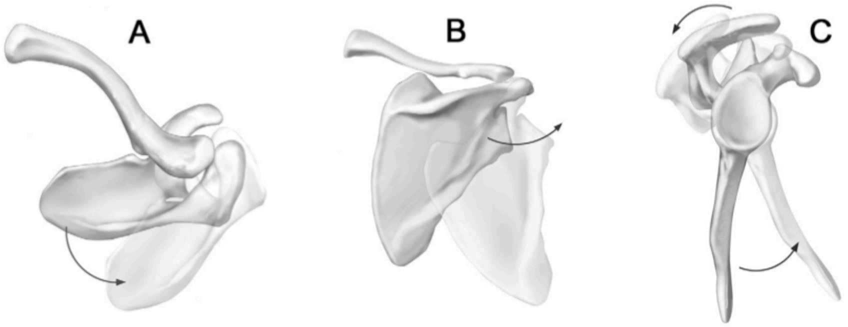


Figure 14: Scapular rotations of protraction/retraction (A), internal/external rotation (B), and anterior/posterior tilt (C). From Ludewig et al., 2004.

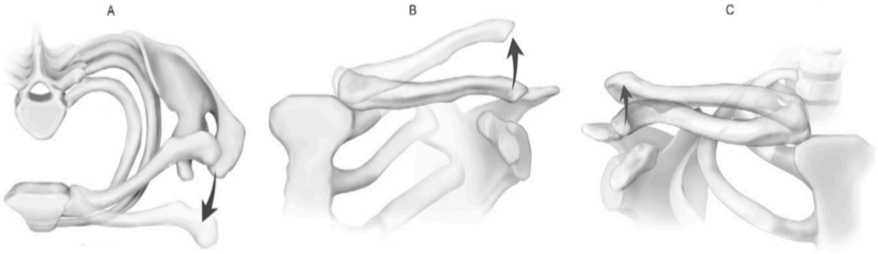
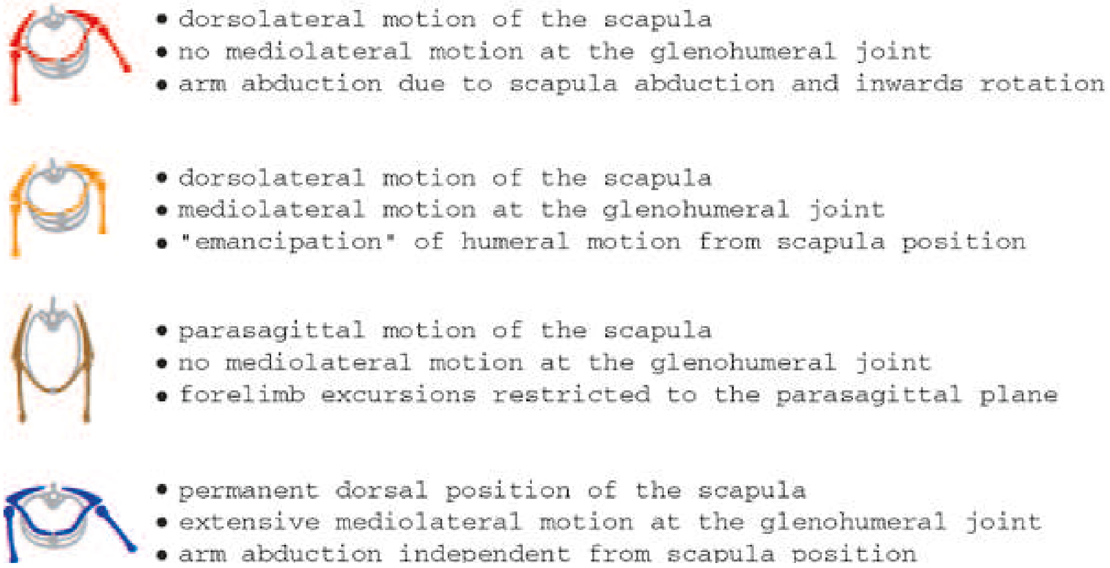


Figure 15: Clavicular rotations of protraction/retraction (A), elevation/depression (B), and anterior/posterior rotation (C). From Ludewig et al., 2004.

There is currently no three-dimensional motion capture of scapular movement, or predicative equations and mathematical characterizations for the shoulder rhythm in chimpanzees. The orientation of the bones that make up the primate shoulder have been analyzed and linked to the range of locomotor and non-locomotor activities performed by primates (Schmidt & Krause, 2011). Features such as clavicle length, scapular length and thoracic shape have associated with specific locomotor behaviors and ranges of motion in non-human primates (Schmidt & Krause, 2011). Work by Schmidt and colleagues (2011) assessed and grouped a large number of primate species based on their known scapular and humeral features and orientations (Figure 16). While scapular motion is considered very similar among a wide variety of primates (Schmidt & Krause, 2011), some important differences exist. In particular, hominids, hylobates and ateles have a very similar scapular motion, including maintenance of a posteriorly positioned scapula (Figure 16). Given these similarities, the gross structure of the chimpanzee shoulder rhythm will be similar to human shoulder rhythm.



- dorsolateral motion of the scapula
- no mediolateral motion at the glenohumeral joint
- arm abduction due to scapula abduction and inwards rotation

- dorsolateral motion of the scapula
- mediolateral motion at the glenohumeral joint
- "emancipation" of humeral motion from scapula position

- parasagittal motion of the scapula
- no mediolateral motion at the glenohumeral joint
- forelimb excursions restricted to the parasagittal plane

- permanent dorsal position of the scapula
- extensive mediolateral motion at the glenohumeral joint
- arm abduction independent from scapula position

Figure 16: From Schmidt & Krause (2011) demonstrating the four different categories of scapular and humeral motion designated for various primates species. Hominids (such as chimpanzees), Hylobates (such as gibbons) and Ateles (such as spider monkeys) all fall into the bottom blue grouping.

Along with the utility of known data on human shoulder rhythm, data exists on closely related primates that can prove informative in inferring chimpanzee shoulder rhythm. Two-dimensional scapular rotations have been examined in small primates, including spider monkeys (*Ateles*), vervet monkeys, squirrel monkeys and lemurs (Jenkins et al., 1978; Schmidt, 2005; Schmidt & Fischer, 2000; Schmidt & Krause, 2011; Whitehead & Larson, 1994). This work on scapular kinematics has mostly been conducted during quadrupedal walking, but can give further insight into the motions of the scapula in a primate upper extremity that is highly involved in locomotion, both terrestrial and arboreal.

2.9.4 Determination of External Forces and Moments

To calculate forces and moments occurring in the tissues of the shoulder, the total external forces and moments occurring at the joints need to be calculated (Dickerson, 2008). This is done using kinematic data, measurement of external forces acting on the body and body segment properties.

A model first needs to define the appropriate segments necessary to answer the research question. To study shoulder biomechanics, a model typically includes the body segments of the thorax, upper arm, forearm and hand. Segments are defined by physical properties such as masses, center of masses, and inertial properties of the upper extremity (Dickerson et al., 2006; Winter, 2009). There are many sources of segment masses in humans, from cadaveric dissections and medical imaging (Durkin & Dowling, 2003; Winter, 2009). Segment properties such as joint centers, centers of mass, and inertial properties are calculated within the model using published regression equations (Zatsiorsky & Seluyanov, 1993). Kinematic motion data is used to calculate joint centers based on geometric assumptions of the location of joint centers from anatomical landmarks and regression equations (Dickerson et al., 2006; Nussbaum & Zhang, 2000). Centers of mass can then be calculated within the model using published data on the spatial locations of center masses and joint center locations to determine segment lengths (Clauser et al., 1969; Dickerson et al., 2006). Analogous segment property data on chimpanzees exist, which can be used to inform a musculoskeletal model (Zilhman, 1992; Thorpe et al., 1999).

Kinematic displacement data from motion capture is used to determine linear and angular velocities and accelerations. Linear velocities and accelerations of segment centers of gravity are determined through numerical differentiation (Dickerson et al., 2006). Angular kinematics are calculated following assessment of angular rotations from the kinematic displacement data, typically using the Joint Coordinate System (Dickerson et al., 2006; Nigg & Herzog, 2007). The Joint Coordinate System is derived from the Euler Angle technique, and determines angular rotations of segments based on orthopaedically relevant joint rotations of flexion/extension, abduction/adduction and rotation about the longitudinal axis of the segment (Nigg & Herzog, 2007). Angular segment velocities and accelerations are determined through the first and second derivatives of the Euler angles (Dickerson et al., 2006; Vaughan et al., 1992).

Combining the segment property data and kinematic data inputs used to determine linear and angular kinematics, and segment properties, Newtonian equilibrium equations based on the second law of motion are applied to determine net joint reaction forces and moments (Dickerson, 2008). Both a linear and angular form of Newton's second law of motion are applied to determine forces and moments, respectively. The linear form of the equation determines forces using segment masses and accelerations of the segment centers of mass, as well as any external forces applied to the system, such as weights of the segments and hand forces (Dickerson et al., 2006). The angular form of the Newtonian equation determines moments using the rate of change of the segmental angular momentum, calculated from segmental moments of inertia, and segmental velocities and accelerations (Dickerson et al., 2006). The output of this process is three-dimensional external forces and moments about each of the modeled joints.

2.9.5 Optimization to Determine Soft Tissue Load Sharing

There are a large number of muscles that cross the joints of the shoulder. Any number of these muscles may potentially contribute to generating net external joint reaction forces and moments. This creates a mechanical indeterminancy problem, where there are more muscles contributing to movement than there are degrees of freedom and conditional system equations to solve for each muscle force (Dickerson, 2008). While so many muscles give the body versatility to perform a spectrum of movement, it also means that there is not one unique solution for load sharing between the muscles (Dul et al., 1984). Experimental electromyography research on humans and chimpanzees has demonstrated intra- and inter-individual patterns of muscle recruitment (Larson & Stern Jr, 2006, 2013; Winter, 1989). Therefore, muscle recruitment to perform a task is not random, but follows a physiologically based decision making process. One approach to solving for a number of unknown muscle forces that exceed the system equations is found through a mathematical optimization routine (Nigg & Herzog, 2007).

Optimization techniques approach the muscle indeterminancy by making the assumption that the body selects muscles to contribute to an overall joint moment according to a physiological criterion (Crowninshield & Brand, 1981). Optimization routines depend on three primary properties: an objective function, design variables, and constraint functions (Nigg & Herzog, 2007). The first property, the objective function, is the parameter that is optimized. It is assumed to be part of a central nervous system operation to minimize or maximize a biological function (Dickerson, 2008). Examples of objective functions include minimizing muscle forces, stresses or fatigue, or maximizing force, speed, or endurance (Crowninshield & Brand, 1981; Dul et al., 1984; Nigg & Herzog, 2007). The chosen objective function is dependent on the specific task being modeling and the theorized physiological basis for completing the task. For example, human bipedal locomotion is believed to be performed in a manner than minimizes energy expenditure, and can serve as the foundation for a physiologically relevant objective function (Crowninshield & Brand, 1981). The second property of an optimization routine is the design variables. These design variables are the output of the objective function, and are systematically changed until the objective function is optimized (Nigg & Herzog, 2007). In the case of a musculoskeletal model, the design variables are the outputted and resultant individual muscle forces. The final property of an optimization routine is the constraint functions. These are inputs that restrict the optimization solution space by providing limits and boundary conditions to the design variables and resulting optimized solution space (Nigg & Herzog, 2007). These can include known information about muscle physiology for individual muscles and kinematic checks on posture. These constraints prevent the resulting muscle forces from falling outside a physiologically realistic range.

Biomechanical optimization routines have successfully modeled human muscle patterns. However, optimization routines are only as realistic as the model design. As full physiological, neurological and biomechanical realism is still difficult to model, optimization is still limited in its capability to consistently and accurately recreate muscle activity patterns (Dickerson, 2008; Nigg & Herzog, 2007). Models must account for numerous musculoskeletal biomechanical and physiological parameters and variables. Accurately representing musculoskeletal physiology and biomechanics has to be balanced with the ability to produce a model that can execute the required outcome (Pandy, 2001).

A physiological parameter of particular relevance to the shoulder is properly accounting for the multifaceted glenohumeral stability in an optimization routine. How each component of glenohumeral stability contributes to joint function is not known. Modeling approaches have to take this into consideration and choose modeling parameters that are, at present, feasible to represent mathematically and physiologically. One important mechanism of instrinsic glenohumeral stability is the concavity and shape of the glenoid (Lippitt et al., 1993). Compression of the humeral head into the concave glenoid fossa provides a large part of the passive joint stability in the mid-range of joint motion (Lippitt et al., 1993). In musculoskeletal models, glenohumeral stability is typically represented by constraining the net humeral joint reaction force vector to be directed into the elliptically shaped glenoid fossa through direction-specific stability ratios (Dickerson, 2008). The stability ratios are derived from experimental cadaveric research that has determined the intrinsic amount of shear force that can be resisted for a compressive force into the glenoid fossa (Dickerson, 2007; Lippitt et al., 1993). Integration of these stability ratios into a musculoskeletal model reflects the intrinsic, passively generated joint stability by computationally restricting contact forces within the glenohumeral joint.

A number of musculoskeletal models exist of the modern human shoulder (Gatti et al., 2007). These models incorporate musculoskeletal data to predict muscle and joint forces and moments during specific upper extremity tasks (Charlton, 2003; Dickerson et al., 2007; Favre et al., 2005; Garner & Pandy, 2001; Holzbaur et al., 2005; van der Helm, 1994). Dickerson and colleagues (2007) developed a dynamic musculoskeletal shoulder model for estimating joint and muscle loads at the shoulder. This model – Shoulder Loading and Assessment Modules (SLAM) – considers kinematic and kinetic effects, geometric realism and population scalability (Dickerson et al., 2007).

2.9.6 Probabilistic Modeling of Variability

Most shoulder models are designed to produce a single set of outputs for a specific set of inputs, making them deterministic by definition (Olofsson, 2005). A deterministic model simulation can be run repeatedly using different input values to produce a range of outputs. Deterministic model outputs thus may represent variability within a sample of simulations or subjects. It does not, however, consider the full range of variability and probability of possible outputs within a population (Olofsson, 2005). Deterministic analyses and models only consider the effect of a specified input on a desired output for specific scenarios.

Uncertainty and variability are highly present in biomechanics and physiology (Laz & Browne, 2010). Biomechanical factors such as kinematics, kinetics, anthropometrics, morphological geometry and properties can vary from person to person (Laz & Browne, 2010). A deterministic analysis does not account for the probability of an outcome, given defined inputs. To produce biofidelic randomness in outputs, a probabilistic model, not a deterministic model, must be created. A probabilistic analysis considers the variability and likelihood of an output by considering realistic ranges of uncertainty in the inputs and model parameters (Laz & Browne, 2010; Oloffson, 2005).

In a probabilistic model, input and model parameters are represented as distributions, as opposed to single representative values (Laz & Browne, 2010). A distribution indicates the likelihood that the input or model parameter will take on a specific value. Characteristics of a distribution can be represented a few different ways. These include a Normal (Gaussian), lognormal, Poisson, binomial and Weibull distribution (Laz & Browne, 2010). The most commonly used in biomechanics is the

Normal (Gaussian) distribution, where the most probable events occur around the mean value, and the tail regions of the distribution represent less probable events (Choi et al., 2007; Halder & Mahadevan, 2000). A normal distribution is symmetric about the mean and bell-curved. With the input distribution known, the probabilistic model can be run to produce a distribution for each of the outputs.

Different methods for generating the distribution for the output variables exist. The Monte Carlo simulation is the most common and often considered the "gold standard" (Langenderfer et al., 2008). A Monte Carlo simulation is an iterative process that will theoretically provide a solution distribution when enough iterations are performed of a deterministic function using the combinations of values obtained through random number generation (Chopp-Hurley, 2015; Langenderfer et al., 2008; Reinbolt et al., 2007). While very accurate, this process is computationally substantial. Alternative methods have been proposed to reduce the intensive computation required through a Monte Carlo simulation, including the Most Probable Point method. Instead of computing the values of every single point of the distribution, the Most Probable Point method determines the input values at identified probability levels, which are then used to derive corresponding outputs (Langenderfer et al., 2008; Mavris & Brandte, 1997). The iteration is repeated for a specified number of probability levels to meet the desired resolution (Mavris & Bandte, 1997). This method has demonstrated comparable results to the Monte Carlo method at a fraction of the computational cost (Chopp-Hurley, 2015; Laz & Browne, 2010).

In biomechanical modeling, a probabilistic model can be created by expanding an existing deterministic model. The desired inputs or internal model parameters only need to be converted into the appropriate distributions, and a probability simulation technique applied to determine the distribution of the output variables. Deciding which input variables or internal parameters to model as distributions depends on the model and research question. The inputs and parameters of interest must be defined. In anthropology and biomechanics, these often are related to morphological variability. Morphology has been deemed to have significant impact on the musculoskeletal function of the primates (Larson, 1995).

2.10 Biomechanical Models of Human Ancestry

Using fossilized remains as the foundation of the approach, a number of researchers have applied biomechanical principles to attempt to model the likely movement patterns of extinct hominins. Like much of the anthropological literature, this work has mostly focused on the lower limb due to the keen interest in the development of human bipedalism. Researchers have attempted to resolve the debate regarding the locomotor behaviors of ancient humans in a number of ways. Biomechanical approaches have included experimental studies on locomotor biomechanics of modern primates and humans, to musculoskeletal modeling of ancient humans and extant apes.

There have been many attempts to resolve the debate surrounding the mechanical effectiveness of bipedal walking in early hominins. Sahelanthropus tchadensis, Orrorin tugenensis, Ardipithecus ramidus, Australopithecus *afarensis* are considered some of the possible earlieest bipedal hominins (Lovejoy et al., 2001; Nagano et al., 2005). Experimental studies of modern humans have demonstrated that a bent-knee, bent-hip gait is mechanically inefficient (Li et al., 1996). But morphological differences between Australopithecus *afarensis* and modern humans confound direct comparisons. A compliant gait pattern could have been more efficient in ancient humans who were transitioning to habitual bipedalism (Crompton et al., 1998). A pair of bipedal footprints created by two ancient hominins approximately 3.5 million years old, are believed to have been created by Australopithecus *afarensis* (Raichlen et al., 2008). Spatial-temporal features of the fossilized footprints alone do not distinguish between the gait postures of modern human and chimpanzee bipedalism (Raichlen et al., 2008). However, a biomechanical comparison of the weight distribution of the ancient footprints to those created by modern humans performing a normal modern gait and a bent-knee bent-hip gait pattern match that of modern humans walking with a normal, extended gait (Raichlen et al., 2010). This lends evidence to Australopithecus *afarensis* having a bipedal gait more similar to modern humans than modern apes (Raichlen et al., 2010).

Computational musculoskeletal modeling has been used to attempt to resolve the debate regarding early bipedal locomotion, using the morphological information contained in the fossilized remains. Due to limited fossilized resources, these models often assume some musculoskeletal model parameters derived from scaled modern human or chimpanzee data. Using the assumption that efficient walking aims to reduce the cost of locomotion, Crompton and colleagues (1998) created a dynamic whole body model of Australopithecus *afarensis* and assessed for lower extremity mechanical joint power in erect bipedal gait and bent-knee bent-hip gait in the sagittal plane. Two models were created – one with mass distributions and inertial properties similar to the modern chimpanzee and one similar to the modern human (Crompton et al., 1998). Only human erect walking and bent-knee bent-hip walking was successfully modeled and produced ground reaction forces typical of those produced by humans in both scenarios. A subsequent two-dimensional dynamic inverse model of the Australopithecus *afarensis* lower extremity constrained the stride lengths of the model to Australopithecus *afarensis* footprints left in Laetoli, Ethiopia 3.5 million years ago (Sellers et al., 2005). The model successfully simulated experimentally derived modern, extended gait postures over a range of walking speeds. Forward dynamics optimization has also shown similar results regarding ancient human locomotion. Muscular activation patterns and lower body kinematics during simulation of bipedal walking in Australopithecus *afarensis* A.L. 288-1 were demonstrably similar to those seen in modern humans despite different bone morphology (Nagano et al., 2004). These results from biomechanical models lend strong evidence to Australopithecus *afarensis* locomoting in a manner that falls within the boundaries of normal modern human locomotion (Crompton et al., 1998; Nagano et al., 2004; Sellers et al., 2005).

Computational modeling of the chimpanzee has been conducted through a three-dimensional lower extremity model. Similar to models of ancient humans, chimpanzee models can be used to compare form and function of the primate to humans to derive conclusions regarding arboreal and terrestrial locomotion associations to musculoskeletal form. Modeling the chimpanzee lower extremity allows comparison between physiological capacity and function in humans and chimpanzees limb muscle function (O'Neill et al., 2013). When compared to an analogous lower extremity human model, a chimpanzee lower extremity model demonstrated reduced force-producing capabilities in the lower extremity, but increased range of motion over which force could be produced at joints such as the ankle. It was hypothesized that the chimpanzee's arboreal locomotion is the primary reason for these differences in muscle physiology, architecture and resultant capability. Chimpanzees are not locomotor specialists like humans (Larson, 2000). They require a greater range of joint motion to perform both arboreal and terrestrial locomotion (Larson, 2000; O'Neill et al., 2013). To produce force through a greater range of motion, chimpanzees developed longer muscle fibers, sacrificing some lower extremity joint power capabilities (Walker, 2009).

These models highlight the utility of modeling chimpanzee and human relative biomechanics and musculoskeletal physiology. Contrasts between chimpanzee and human models can help identify the specificity of the musculoskeletal system for each species. Many of these comparative lower extremity models have demonstrated the association between musculoskeletal leg form and function. Computational models present the effect of muscle physiology and morphology on joint kinematics and kinetics between the two species with lower extremity models identifying the physiological and biomechanical features that have made human bipedalism an efficient and useful modern adaptation. Utilizing the scientific and musculoskeletal data on modern chimpanzees, researchers have exploited the morphology, physiology and biomechanics of the closest living relative to humans to further anthropological work in human evolution and modern human function. This research can inform the possible transition from arborealism to bipedalism in humans. In particular, comparative evolutionary models can quantify musculoskeletal differences that elucidate modern human upper extremity strengths, limits and injury risk. While models exist of the lower extremity, no attempts have been made to model the upper extremity to draw quantitative lines between form and function.

2.10.1 Comparative Anthropological Biomechanical Modeling of the Shoulder

Compared to the lower extremity, there has been limited research on upper extremity evolution. Comparative morphological studies have been conducted between modern and ancient humans and primates. Experimental studies have been conducted on primates, analyzing kinematic and kinetic differences between species. But to date, no musculoskeletal models have been developed to analyze the physical capabilities of primates or ancient humans, compared to modern humans.

The lack of biomechanically driven anthropological analyses of the shoulder has left a gap in human evolutionary and functional study. Despite its somewhat modern human gait mechanics, Australopithecus *afarensis* still appears to have retained some morphological features for arborealism that may have impeded striding bipedalism (Crompton et al., 1998; Green & Alemseged, 2012). The arm swing is integral to the ability to walk bipedally and maintain balance (Alexander, 2004). There are no existing biomechanical models of the upper extremity of chimpanzees or ancient human species that attempt to determine biomechanical capacity as it relates to modern human capacity. To fully support evolutionary hypotheses regarding lower extremity bipedality, it is imperative to also understand accompanying upper extremity function evolution. Biomechanical models are one avenue to explore and understand the function and capacity of the upper extremity. Determining whether ancient human shoulder function was primarily arboreal like a modern chimpanzee or non-locomotor like a modern human will help clarify theories of the human evolutionary pathway to modern human locomotion, behaviors and limitations.

A computational biomechanical model of a brachiating upper extremity can be developed through extension of the knowledge and theoretical basis behind current modern human shoulder models. As discussed previously, one such model is the

University of Waterloo's Shoulder Loading Analysis Modules (SLAM). While developed for ergonomic purposes, SLAM provides broad outputs that can be used to describe the general physical capabilities of the shoulder in modern humans. Models such as this can be revised to represent the upper extremity of another primate or ancestral species with arboreal capacity. Comparisons between outputs of the modern human model and an analogous comparator model will elucidate which morphological features affect arboreal upper extremity capacity.

The chimpanzee shoulder represents a highly viable comparative model for understanding evolution of the human shoulder. Chimpanzees are the closest genetic living relative to humans, and as such share similar shoulder structure and function (Young et al., 2015). Both species share a gross shoulder structure and form. Though specific differences exist which help to delineate the two, both have shoulder bone shape that defines the great ape morphotype as distinct from other primates (Larson, 1998; Young 2003, 2008). Humans and chimpanzees also have most of the same musculature comprising the shoulder, with similar origins and insertions (Swindler & Wood, 1973). Resultantly, both species have a large amount of functional overlap at the shoulder. However primary shoulder function is highly divergent between humans and chimpanzees. Like humans, chimpanzees perform non-locomotor tasks with their upper extremity. These include throwing, carrying and reaching, tool creation and use, and communication (Cartmill & Smith, 2009). However, humans are much more proficient at these tasks than chimpanzees. The non-locomotor proficiency of the human upper extremity has often been highlighted as integral to human survival and prosperity. It many, however, also be tied to the human predisposition for fatigue- and impingement-related rotator cuff pathologies. Conversely, chimpanzees are more proficient in locomotor behaviors that utilize the upper extremity, such as terrestrial quadrupedalism and brachiation. While humans can perform locomotor behaviors such as climbing, and may have ancestral ties to them, the modern efficiency, comfort and sustainability is limited. Exploring an ancestral locomotor climbing task could give insight into human shoulder pathology by highlighting the biomechanical limitations of the modern human shoulder in an extreme exposure. Along with their similarity to humans, chimpanzees also represent one of the better documented comparator species. Along with musculoskeletal dissections characterizing skeletal form and orientation, and muscular mass and architecture, chimpanzee muscle activity and body motion has been characterized in a variety of tasks, including reaching, and terrestrial and brachiation locomotion. This breadth of data provides greater opportunity to make direct comparisons with humans.

Musculoskeletal modeling of chimpanzee behavior and locomotion can also inform potential evolutionary adaptations of human locomotion. Probabilistic modeling can give greater insight into the effect of morphological variability on variation in musculoskeletal function. Chimpanzees represent the strongest living link to the human evolutionary history. Given evidence that humans and chimpanzees arose from a common ancestor, their physical morphology and behaviors may help explain how humans evolved their unique musculoskeletal form (O'Neill et al., 2013). If humans were ever arboreal and, subsequently became modern beings with limited overhead, weight-bearing abilities, what musculoskeletal features dictated these modifications in capability is unknown. Comparison with the closely related, structurally and functionally similar, and well documented chimpanzee would be an appropriate first step to identifying distinctive human musculoskeletal traits that dictate modern function and injury risk. The chimpanzee represents a musculoskeletal system that shares overall functional shoulder ability, but retains an ancestral arboreal and brachiating capacity that is greater than in modern humans. Within a comparison with chimpanzees could rest the explanation for what distinguishes human function and pathology, and the unique upper extremity evolution of humans since divergence from a common ancestor with chimpanzees. Biomechanical musculoskeletal models present the opportunity to quantify and understand which musculoskeletal features of the upper extremity are associated with the ability to be arboreal, and to successfully brachiate. In turn, this will inform biomechanical theories regarding the manifestation of unique human upper extremity capabilities and overhead injury mechanisms.

Chapter 3 Study 1: Kinematic and EMG analysis of brachiation in humans

3.1 Introduction

In the search for knowledge of human origins, anthropologists and zoologists have documented and quantitatively analyzed the movement of animals such as chimpanzees and other great apes. This has led to a greater understanding of animal social and feeding behaviors, locomotion, physical abilities and biomechanics (Stevens & Carlson, 2008). Analysis of primates has also highlighted numerous commonalities and differences between humans and their closest living relatives, and aided understanding of the range and limits of the modern human body.

The human shoulder has become adapted for many different locomotor and non-locomotor behaviors, which differentiate them substantially from other primates. Humans possess generally mobile and unstable shoulders like chimpanzees, but are unable to maintain sustained overhead postures like chimpanzees (Wood & Richmond, 2000). The human upper extremity is involved in activities such as arm swinging during gait, tool manipulation, carrying and throwing (Wood & Richmond, 2000). While the closely related chimpanzees perform many of these activities less often and less skillfully than humans, they also spend substantial time with their upper extremity in overhead positions for reaching, brachiation and hanging behaviors (Stern & Larson, 2001). The non-locomotor usage of the human upper extremity is typified by less power. It has muscle insertions that produce less force output and boney orientations that are not designed for elevated postures and power, but instead for better fine motor control (Lewis et al., 2001; Thorpe et al., 1999; Wood & Richmond, 2000). This makes the human upper extremity less adapted for overhead behaviors and susceptible to pathology in this posture (Lewis et al., 2001; Wood & Richmond, 2000).

Humans and chimpanzees likely have a common arboreal ancestry, making the kinematics and kinetics of arboreal behaviors like brachiating arm swinging in chimpanzees and humans of anthropological interest (Green & Alemseged, 2012; Larson, 2007; Young & Roach, 2015). Biomechanical analyses of chimpanzee behaviors such as brachiating and hanging exist, as well as studies of chimpanzees performing terrestrial locomotion and some human-like tasks including bipedalism and reaching (Larson & Stern, 1986; Larson et al., 1991; Stern & Larson, 2001; Usherwood et al., 2003). No parallel biomechanical studies exist examining humans performing brachiation, mimicking proposed ancestral behaviors. However, many studies have examined the effect of overhead upper extremity postures on the human musculoskeletal system.

Arboreal behaviors in humans are also of biomechanical and clinical interest. Overhead arm postures are particularly problematic for humans, in contrast with chimpanzees. Brachiation is similar to an overhead reach, in that it is comprised of arm flexion, abduction and axial rotation (Larson, 1988). However, in humans, overhead postures increase the physical loading of soft tissues of the upper extremity (Ebaugh et al., 2006; Grieve & Dickerson, 2008; Lewis et al., 2001; Rashedi et al., 2014). The high musculoskeletal demands placed on the human shoulder joint during overhead tasks make this a particularly difficult posture to maintain (Rashedi et al., 2014). As such, sustained and repetitive overhead postures lead to rapid fatigue of the shoulder muscles (Dickerson et al., 2015; Ebaugh et al., 2006; Rashedi et al., 2014). These postures become even more problematic as workload increases or the posture is sustained for longer periods (Ebaugh et al., 2006). Elevated, overhead postures have also been associated with the development and progression of subacromial impingement syndrome, defined as pain and dysfunction resulting from pathology of any of the structures in the subacromial space (Lewis et al., 2001). As the arm elevates, the subacromial space decreases, reducing the space through which the supraspinatus tendon passes and increasing risk for impingement (Bey et al., 2007; Graichen et al., 2001). Conversely, chimpanzees regularly assume and maintain low and high force overhead postures without developing shoulder pathology (Cartmill & Smith, 2009; Potau et al., 2007;

Stern & Larson, 2001). Despite a likely arboreal common ancestor with chimpanzees, the human shoulder appears to have devolved its ability for overhead postures.

Modern human brachiation performance has not been objectively and biomechanically investigated, despite the behavior's relevance to human evolution and modern shoulder musculoskeletal form and function. It is unknown how humans might conduct ape-like behaviors such as overhead arm swinging. Brachiation postures, in which the weight of the entire body mass is often supported by the shoulder, require powerful and prolonged activity from the muscles of the shoulder girdle (Lewis et al., 2001). Prolonged brachiating through arm swinging and overhead hanging will likely cause muscle fatigue and cause kinematic compensatory behaviors. After repeated exposures, this would probably lead to musculoskeletal disorders such as subacromial impingement and rotator cuff tears (Lewis et al., 2001). Data on humans in brachiating postures can be used to compare the physical and biomechanical differences between humans and chimpanzees in upper extremity capabilities and demand, and to better understand the musculoskeletal limits of the human shoulder.

3.2 Purpose

The purpose of this study was to examine right-side human kinematics and select electromyographical activity in experienced and inexperienced climbers during horizontal bimanual arm-suspension climbing, intended to mimic brachiation behaviors in chimpanzees. The human video and electromyographical data was compared with extant datasets for chimpanzees to assess differences between species in kinematics and muscular activity. Kinematic brachiation data collected in this study subsequently served as inputs to the SLAM musculoskeletal model of the human shoulder. The study is outlined in Figure 17.

3.3 Hypotheses

Data analyses were comprised of experienced and inexperienced human climbers, and humans and chimpanzees comparisons. As such, hypotheses are divided by two the two comparative analyses.

3.3.1 Between Human Climbing Groups

Hypothesis one - Inexperienced climbers will use different kinematic techniques, including increased thoracohumeral elevation and decreased elbow flexion to create forward momentum.

Hypothesis two - All participants will sustain shoulder musculature activation at or above 25% maximum voluntary exertion for most of the climb cycle to maintain the climbing postures, particularly in support phase.

Hypothesis three - Inexperienced non-climbers will activate all muscles at a higher proportion of capacity throughout the climb cycle to compensate for less familiarity with climbing.

3.3.2 Between Species Groups

Hypothesis four – Despite morphological adaptations away from overhead postures and climbing, humans will use similar kinematic patterns as other primates to performing a similar climbing task.

Hypothesis five - Owing to their common ancestry, humans will share common overall muscle activation timing patterns with chimpanzees while performing a similar climbing task.

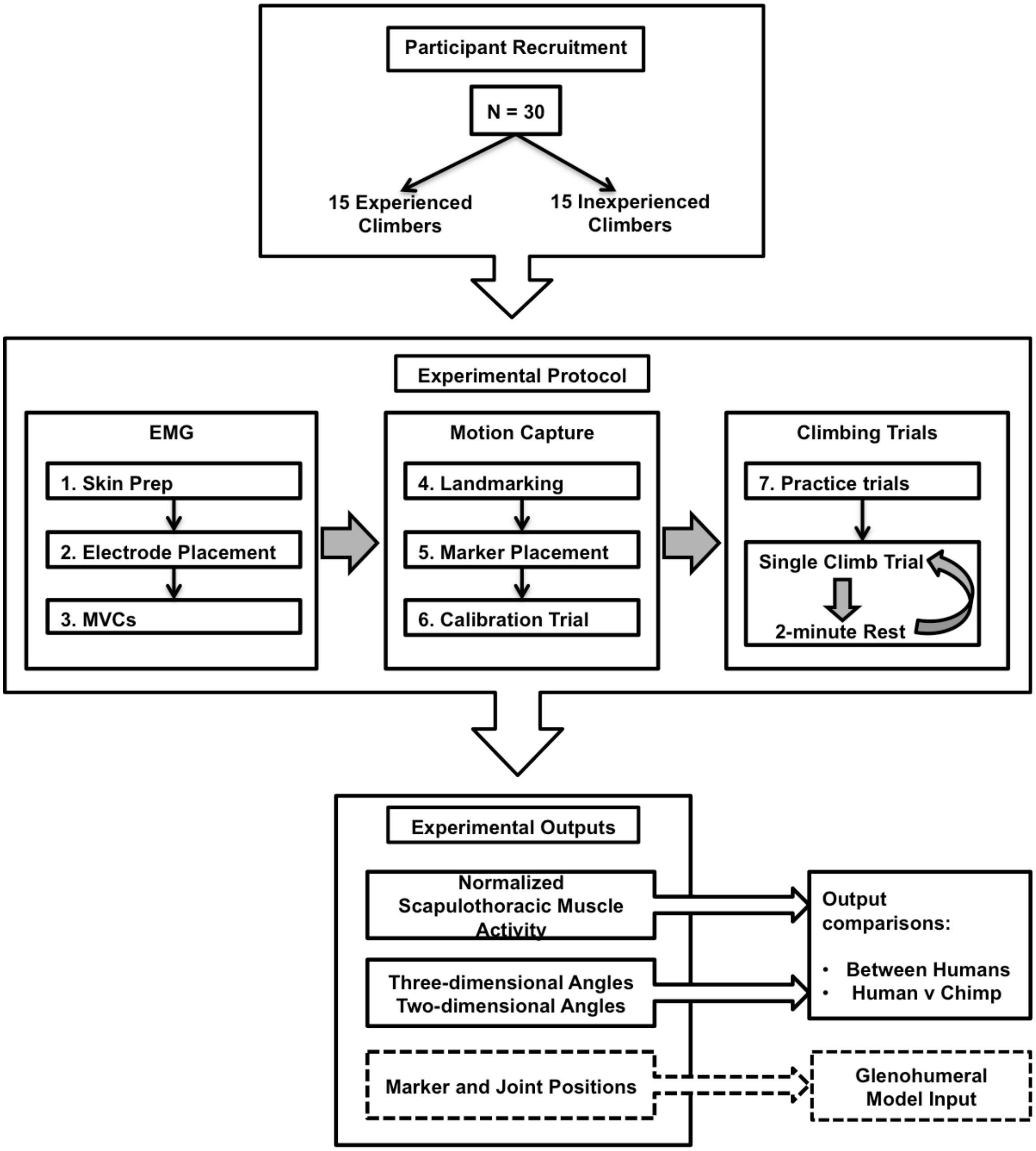


Figure 17: Overview of Study 1 of the thesis, human brachiation experiment. 30 human participants will follow a right-side EMG and motion capture protocol and complete a horizontal climbing task. This data will be compared between human participant groups, and will also be qualitatively compared to available chimpanzee climbing data. The kinematic output, highlighted in dashed boxes, will also be used as an input for the glenohumeral model in subsequent studies.

3.4 Methods

Right-side comparisons between two human participant groups, and between humans and chimpanzees, were made for several outputs from a bimanual arm-swinging task. The set up for collecting human bimanual climbing data followed methodologies used in previous work conducted by researchers examining ape kinematics and kinetics during brachiation. This intended to enable comparisons between primate studies and the present human study. Motion capture was used to analyze kinematics of human climbing. Electromyography was collected to analyze muscular activity during human climbing.

The study was approved by the University of Waterloo Research Ethics Board and all participants provided informed consent.

3.4.1 Climbing Apparatus

A TRX suspension training system was used as the support structure for the climbing task. Eight rungs were attached to the TRX system (Figure 18) in horizontal sequence, equally spaced 40 centimeters apart (Stern & Larson, 2001). This created a horizontal ladder apparatus for the climbing tasks. The rungs were located 2.2m off the floor.

Figure 18: Image of a study participant performing the climbing task on the climbing apparatus. Rungs were affixed to a TRX suspension training system. The participant alternated the support hand for each upcoming rung. The eight rungs used as climbing supports were attached to a TRX.

3.4.2 Participants

30 participants were recruited from the University of Waterloo population, 15 experienced climbers, and 15 inexperienced non-climbers, with 12 males and 3 females in each group. To qualify as a climber, participants were required to have at least 2 years of climbing experience and partook in climbing activities regularly, at least once every two weeks. Non-climbers were classified into the participant group if they had never, or only participated in climbing activities a few isolated times. The climbing task was likely to be taxing to many or all participants. To avoid potential injury, all participants were asked about their upper extremity strength and fitness, confidence in their ability to complete the climbing task, and given the opportunity to practice the task. Only those that had high confidence in their ability and displayed moderate proficiency in the task were included in the study. This meant that both participant groups were of a high task competency and fitness level.

3.4.3 Electromyography

Surface electrodes were placed on the right side over the anterior deltoid, posterior deltoid, pectoralis major clavicular and sternal head, supraspinatus, infraspinatus, upper trapezius, middle trapezius, latissimus dorsi, serratus anterior, biceps brachii and triceps brachii following standard placement guidelines (Table 2). A reference electrode was placed on the sternum. Prior to electrode placement, the skin over each muscle belly was prepped by shaving hair and cleansing the area with isopropyl alcohol. Electromyography was collected using a wireless Noraxon TeleMyo 4200T G2 (Noraxon, 2 USA Inc., Arizona, USA) sampled at 3000Hz.

3.4.3.1 Maximum Voluntary Isometric Exertions

Maximum voluntary isometric exertions (MVE) were completed on all right-side muscles collected, prior to the practice time and climbing protocol. This data was used to normalize EMG. Two MVEs were conducted for each muscle as described in Table 2. Each MVE was 5 seconds in length. A rest period of at least 2 minutes was given between each MVE.

Table 2: Electrode placement and maximum voluntary exertion protocol for each of the collected muscles

Muscle	**Electrode Placement**	**MVE Action**
Pectoralis major (clavicular)	Between sternoclavicular joint and the caracoidus process, 2 cm below the clavicle (on an angle down and laterally).	With shoulder horizontally abducted and externally rotated to 90° and elbow flexed to 90° (fingers point to ceiling), horizontal adduction is resisted.
Pectoralis Major (Sternal)	6 cm above the nipple.	With shoulder horizontally abducted to 30° with elbow flexed to 90°, horizontal adduction is maximally resisted.
Anterior Deltoid	2–4 cm below the clavicle, parallel to muscle fibres	With the shoulder flexed to 90°, maximally flex against resistance applied by a research assistant
Posterior Deltoid	2 cm below lateral border of scapular spine, oblique angle toward arm (parallel to muscle fibers).	With shoulder abducted to 90° and externally rotated, and elbow flexed to 90° (fingers point to ceiling), extension is resisted
Supraspinatus	Midpoint and 2 finger-breadths superior to scapular spine	With shoulder abducted 5° and elbow extended (thumb pointing up), abduction is maximally resisted.
Infraspinatus	Parallel to spine of scapulae, approximately 4 cm below, over the infrascapular fossa.	With arm at side and elbow bent to 90°. External rotation of the arm is maximally resisted.
Upper Trapezius	2/3 on the line between the trigonum spinae and the 8th thoracic vertebrae, 4 cm from muscle edge, at approximately a 55° oblique angle.	With head turned to right side, subject resists shoulder abduction at 90° with elbow extended (thumb down to floor).
Middle Trapezius	Placed at 50% of the distance between the medial border of the scapula and the spine, at the level of T3, over the muscle belly	With elbow extended and the shoulder placed in 90 degrees abduction and lateral rotation, subject resists shoulder abduction.
Latissimus Dorsi	6 cm below the inferior angle of the scapula.	With shoulder horizontally abducted and externally rotated to 90° and elbow flexed to 90° (fingers point to ceiling), adduction is resisted.
Serratus Anterior	Below 5th rib, anterior to the latissimus dorsi	In a push-up position, subject anteriorly curls their thorax and protracts their scapula
Biceps Brachii	Above the center of the muscle, parallel to the long axis	With the elbow flexed to 90°, subject resists flexion maximally
Triceps Brachii	On the anterior portion of the upper arm, located medially	With the elbow flexed to 90°, subject maximally resists extension.

3.4.4 Motion Capture

Eight Vicon MX20 infrared cameras (Vicon, Oxford, UK) were used to collect three-dimensional thoracic, clavicular, scapular, upper arm and forearm motion at a sampling rate of 50 Hz. Seventeen passive reflective markers were placed on right side upper extremity landmarks – 7th cervical vertebra spinous process (C7), 8th thoracic vertebra spinous process (T8), suprasternal notch (SS), xyphoid process (XP), medial (ME) and lateral (LE) epicondyles, ulnar (US) and radial (RS) styloids, 2nd metacarpophalangeal, 5th metacarpophalangeal, left and right acromion (AC), left and right anterior superior iliac spine (ASIS), left and right posterior superior iliac spine, and the 5th lumbar vertebra spinous process (L5). In addition, two three-marker clusters affixed to rigid plates were placed on the upper arm and forearm to track upper arm and forearm movement, respectively (Figure 19).

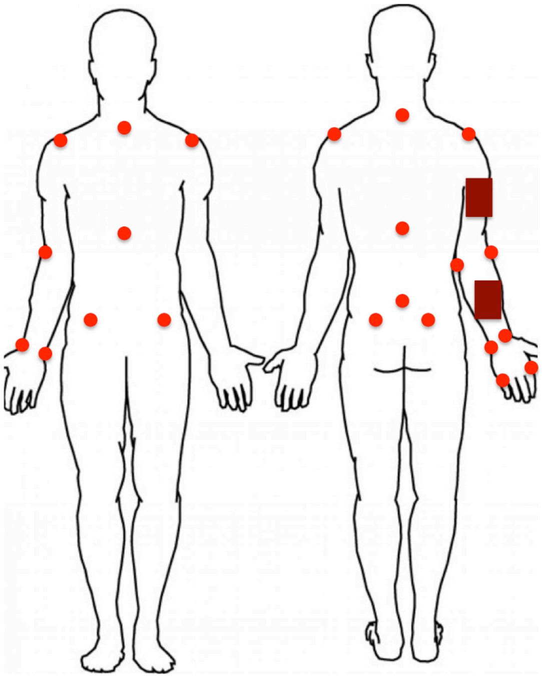


Figure 19: Anterior (left) and posterior (right) view of marker set up, including the arm and forearm marker clusters. Only the right arm was tracked with motion capture markers.

Prior to the climbing protocol, an anatomical calibration trial was collected to establish a relationship between the marker clusters and seventeen calibration markers placed over the anatomical landmarks.

3.4.5 Experimental Protocol

The experimental protocol was the same for all study participants. EMG electrodes were applied and signal tested first, followed by two rounds of MVE trials. Once EMG calibration and MVEs were complete, motion capture markers were affixed to the participant on boney landmarks and a calibration trial was performed. Following motion capture calibration trials, participants conducted the overhead bimanual climbing protocol using the climbing TRX apparatus (Figure 18). For each trial, participants began at one end of the climbing apparatus and were asked to swing across all eight rungs, alternating the contact arm with each ladder rung (Figure 20). Participants were given time to orient themselves to the apparatus and the task, and the opportunity to perform practice trials. Rest periods of approximately 2 minutes were also provided between each climbing attempt. Participants climbed at their own pace. Each participant was asked to traverse the ladder apparatus at least five separate times. When consented to by the participant, video was also taken of the climbing trials.

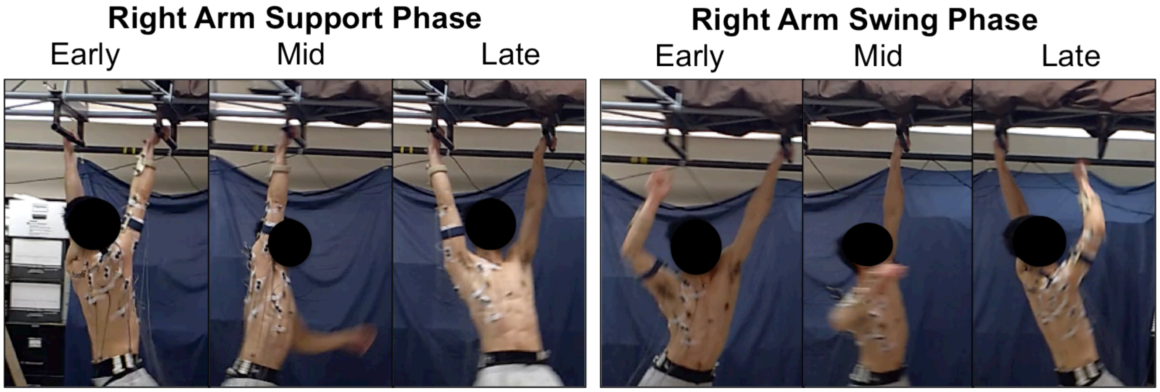


Figure 20: A full, right-arm climb cycle included a support phase followed by a swing phase. Early support beings once the right arm makes contact with a rung. In mid-support the right arm is the sole support limb, as the left-arm is in swing phase. Following late support, the right hand releases from the rung, and right-arm swing phase beings until the right hand makes contact with the next sequential rung.

3.5 Data Processing

EMG and kinematic data was processed using custom-built MATLAB (Mathworks, USA) programs. Each participant had between 5 and 7 climbing trials. Each trial contained one or two full right arm swings that were extracted. A full right arm swing represented right-hand contact with a rung to a subsequent right arm contact with another rung. Each climb cycle included both a “support” phase and a “swing” phase (Figure 20). Support phase represented the part of the cycle where the right arm was in contact with the rung. Swing phase represented the part of the climb cycle where the right arm swung toward the next rung.

The timing of each right arm climb cycle was determined using hand acceleration. The beginning of the right arm support phase was identified as the point when the hand markers, MCP2 and MCP5, reached an acceleration of zero. This time point signified the start of one climb cycle, and the subsequent zero acceleration time point concurrently identified the end of that climb cycle and the beginning of the next climb cycle. Climbing trials were then divided into full right-arm climb cycles for data processing and analysis.

3.5.1 EMG Processing

EMG was high pass filtered at 30Hz to remove potential heart rate and motion artifact (Drake & Callaghan, 2006). The signal was linear enveloped with a single-pass Butterworth low pass filter at 4 Hz (Mathiassen et al., 1995). From the two filtered MVE trials for each muscle, the peak value was extracted to determine the maximum activation for each muscle. This peak MVE value for each muscle was used to normalize each muscle to percent MVE.

The EMG signal for each muscle was normalized to its respective MVE through a right arm swing cycle, from initial contact of the right hand with a rung, through to a subsequent right arm contact with a rung. Each signal was then time-normalized to 100% of the climb cycle, from initial right arm contact with the rung (0%) to the subsequent ipsilateral right arm contact (100%). All the time-normalized trials for each participant were averaged together to produce a single mean climb cycle trial for each muscle. These mean waveforms were used as representative of each participant to perform the statistical data analysis.

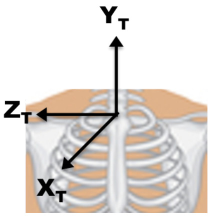
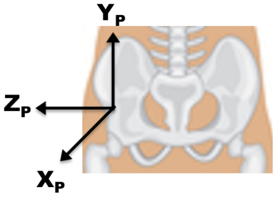
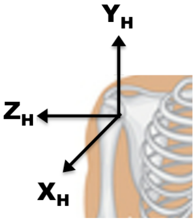
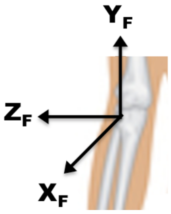
3.5.2 Kinematic Processing

Data was initially processed using Vicon Nexus software (Vicon, Oxford, UK) to properly label all markers and reconstruct any missing marker trajectory data. Data was then dual-pass filtered with a Butterworth low-pass filter at a cut-off frequency of 6 Hz (Winter, 2009).

Four body segments were tracked in the present study – the right forearm, right upper arm, thorax and pelvis. Collection of scapular kinematics was attempted in the present study, using the acromion cluster method (Grewal et al., 2017; van Andel et al., 2009. Due to limitations in the collection space – including a maximum of eight cameras to monitor markers over a 4m space, obstruction from the TRX system, and physical distractions in the collection environment in the view of the Vicon cameras – and the postures used to complete the climbing task, there was too much marker occlusion to adequately track scapular motion. Therefore, scapular motion was excluded from the kinematic analysis.

Local coordinate systems (LCS) were defined for each body segment using global positions of three non-collinear anatomical reflective markers on each segment during the static calibration trial. Coordinate systems followed recommendations and definitions outlined by the International Society of Biomechanics (Johnson et al., 1994; Wu et al., 2005). LCS were created for the right forearm, right humerus, thorax, and pelvis using the anatomical landmark positions in the global laboratory system. An additional landmark was created to represent the glenohumeral (GH) joint center, which also represented the third landmark on the humerus segment. This was defined as 50mm below the acromion (Nussbaum & Zhang, 2000) along the long axis of the thorax. Table 3 shows the anatomical landmarks and coordinate systems used to make each upper extremity LCS.

Table 3: Determination of LCS for each segment, as recommended by ISB (Wu et al., 2005).

Segment	Local Coordinate System
Thorax $X_TY_TZ_T$ 	Y_T: Line connecting the midpoint between XP and T8 and the midpoint between SS and C7, pointing up Z_T: Line perpendicular to the plane formed by SS, C7 and midpoint between XP and T8, pointing lateral X_T: Common line perpendicular to the Y_T axis, pointing forward.
Pelvis $X_PY_PZ_P$ 	Z_P: Line parallel to the line connecting the right and left ASISs, pointing right X_P: Line parallel to the line lying in the plane defined by the two ASISs and the midpoint of the two PSISs, orthogonal to Z-axis, pointing anteriorly Y_P: Line perpendicular to both X and Z, pointing cranially
Humerus $X_HY_HZ_H$ 	Y_H: Line connecting GH and the midpoint of the ME and LE, pointing up X_H: Line perpendicular to the plane formed by ME, LE and GH, pointing forward Z_H: Common line perpendicular to the Y_H- and Z_H-axis, pointing lateral.
Forearm $X_FY_FZ_F$ 	Y_F: line connecting US and midpoint of ME and LE, pointing up X_F: Line perpendicular to plane through US, RS, and the midpoint between ME and LE, pointing forward Z_F: Common line perpendicular to the X_F and Y_F-axis pointing to the right.

The LCS for the right humerus, right forearm thorax, and pelvic segments were used to determine intersegmental angles using relative rotation matrices. The angles described were the elbow (forearm relative to humerus), thoracohumeral (humerus relative to thorax) and lumbar (torso relative to pelvis). All intersegmental descriptions and three-dimensional rotations were based on Euler rotation sequences recommended by the International Society of Biomechanics (Wu et al., 2005). The elbow and lumbar intersegmental angles were described with a Z-X-Y Euler rotation sequence, the thoracohumeral intersegmental angles with a Y-X-Y sequence (Wu et al., 2005).

Like the EMG data, kinematic data was time normalized from right arm contact with a rung to the subsequent right arm contact with a rung. All normalized climb cycles were combined within each participant to create a mean representative climb cycle waveform for each participant. The mean curves for each participant were used to run the statistical data analysis.

3.5.3 Two-dimensional Climbing Video Kinematics

Data collected on brachiating chimpanzees has been largely qualitative. Studies have used video and simple, single-marker motion analyses to examine climbing measures on single subjects (Larson, 1988; Stern & Larson, 2001; Usherwood et al., 2003), and reaching (Reghem et al., 2013). Direct, quantitative comparisons between species was not possible using available chimpanzee data, and the human data collected here. However, video was taken of some human participants climbing in the present study, and video of chimpanzees performing bimanual climbing was donated by the Department of Anatomy at Stony Brook University, New York. This provided an opportunity to perform a two-dimensional video comparison between species in gross climbing kinematics (Figure 21).

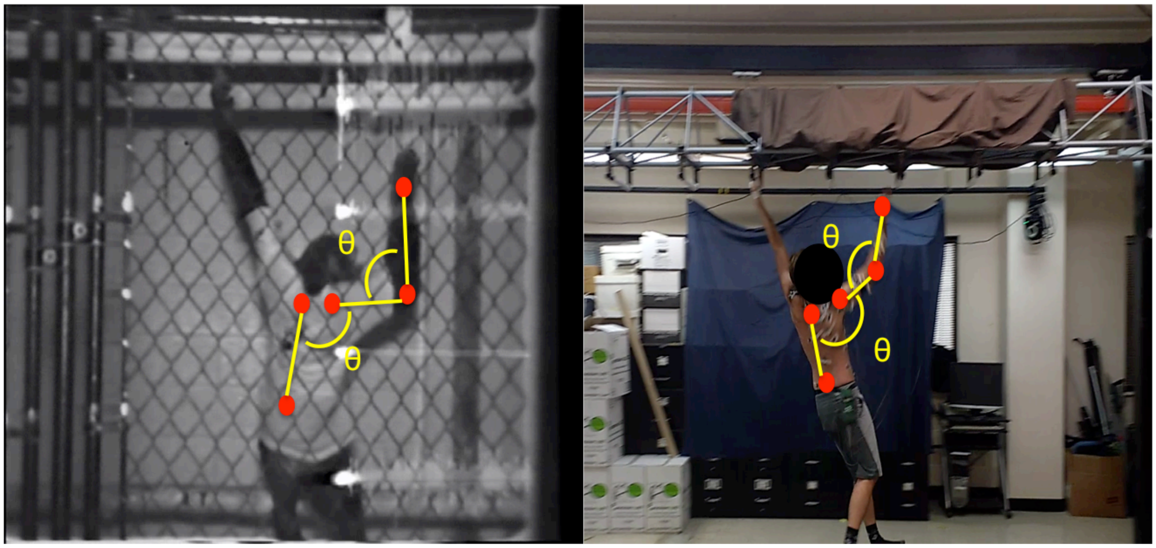


Figure 21: Images taken from video of a chimpanzee climbing (left) and a human climbing (right). The red dots represent the anatomical landmarks that were digitized – L5, C7, humeral head, elbow and wrist. Two-dimensional joint angles derived from landmarks are shown in the yellow θ.

3.5.3.1 Human Data for Two-Dimensional Comparison

The human climbing task was purposely designed to mimic the chimpanzee climbing studies, as a horizontal bimanual arm-suspension climbing task with rungs spaced 40cm apart. The chimpanzees skipped a rung with each arm swing (Figure 21). This alteration of the climbing task was not required of the human participants in the present study. However, each participant was asked if they felt they could perform the climbing task while skipping a rung. A few participants were able, and video was captured of them performing the altered, rung-skipping climbing task. This mimicked the climbing task performed by chimpanzees in the video provided by Stony Brook University, New York and was used to compare the species two-dimensional climbing kinematics (Figure 21).

3.5.3.2 Data Collection and Processing

Full right-arm climb cycles were visually identified on the videos. For a climb cycle, five anatomical landmarks were grossly landmarked and digitized in each video frame of the full cycle – wrist, elbow, humeral head, 7th cervical vertebrae (C7) and 5th lumbar vertebrae (L5) (Figure 21). The two-dimensional coordinates of the landmarks were recorded for each video frame of climb cycle data. The data was used to create a two-dimensional forearm, upper arm and torso, from which a two-dimensional elbow angle and thoracohumeral angle could be calculated using trigonometry (Figure 21). The elbow and thoracohumeral angles were mostly representative of flexion/extension and elevation, respectively (Figure 21). The angles were time normalized to 100% of the climb cycle.

3.6 Data Analysis

The data collected in this study characterizes human brachiation capabilities and strategies through a bimanual climbing task, and compares it between experienced and inexperienced climbing humans, and to chimpanzees. This analysis includes characterization and contribution of the measured shoulder muscles and intersegmental angles to the climb task.

Differences between the two human participant groups were performed using quantifiable statistical analyses. Anthropometric differences between participant groups were assessed using independent t-tests. EMG and kinematic group differences were assessed using a two-way ANOVA approach to parse out the differences between the two participant groups across the entire time-normalized climb cycle. A series of two-way (group and time) ANOVAs ($\alpha=0.05$) were run to determine differences between participant groups across the entire time cycle for each of the joint angles and muscles. Time represented each of the 100 discrete normalized time points in the whole climb cycle. Time was included as a 100-point factor in the ANOVA to assess the accrual of group differences across the whole climb cycle, as opposed to at a single discrete point. Therefore, accumulation of changes in the amplitude over the entire time of the climb cycle, and the possibility of an interaction effect between the whole climb cycle time and participant groups were considered.

A more qualitative approach was taken to analyze between species differences in kinematic strategies and muscle activity. Pseudo-variability was given to the two-dimensional human angles derived from video, using the calculated variability from the three-dimensional kinematics for elbow flexion/extension and thoracohumeral elevation. The variability created the bands of two standard deviations around the human data. Two standard deviations represented 95% confidence interval for the human angles, and a posited range of angles for the human population (Miller, 2006). The chimpanzee waveform was plotted over the 95% confidence interval of the human data. If the chimpanzee waveform fell within the bounds of the human confidence interval, then it could be concluded that the chimpanzee angles are no different than the predicted population-level human angles. The result of this analysis could be used to infer whether horizontal bimanual arm-suspension climbing kinematics would be different between species. The results of this analysis would also be useful for subsequent three-dimensional comparative analyses. If the chimpanzee data falls within the human population confidence interval, human three-dimensional motion data could be considered representative of both humans and chimpanzees, when three-dimensional chimpanzee motion data is non-existent.

Finally, a visual comparison was done between human and chimpanzee EMG to determine if timing of muscle activation was different between species. This comparison was not direct and was only conducted on muscles that have been published on chimpanzees performing the same horizontal bimanual arm-suspension climbing task as the humans in the present study (Larson & Stern, 1986; Larson et al., 1991). While the task both species completed was very similar, there were methodological differences between the chimpanzee and human data collections. The chimpanzee EMG was indwelling, unlike the surface EMG used in the present study. Amplitude normalization to MVE is not possible in chimpanzees, so the amplitudes reported represent amplitude normalized to a maximum recorded EMG (Larson et al., 1991). As such, the EMG comparison between species focused on phasic timing of bursts of muscle activity. This analysis determined if chimpanzees and humans activated muscles at similar times for the same task, and were thus using the shoulder musculature in a similar manner to complete the climbing task.

3.7 Results

The sample analyzed in this study infers brachiation biomechanics in young healthy human adults. Participant group descriptive statistics are presented first. Between human participant group kinematic and muscle analyses are presented next. EMG and kinematics are presented in waveform as descriptive statistics of human kinematics, and muscle contribution and strategy in bimanual climbing. Average between-participant-group statistical differences in intersegmental angles and muscle EMG are also presented. Finally, differences between species are presented. The two-dimensional kinematic video analysis is presented, showing kinematic differences between species. A qualitative comparison of EMG activation timing between species is also conducted (Larson & Stern, 1986; Larson et al., 1991).

3.7.1 Participant Group Anthropometrics

Table 4 shows group differences in subject anthropometrics. No significant differences existed between the participant groups, through the non-climbers were heavier (Table 4).

Table 4: Anthropometrics for both participant groups. Arm span was from tip of fingers to shoulder. Arm girth was taken at the widest part of the upper arm.

	Climbers	Non-climbers	p-value
Sex (M/F)	12M/3F	12M/3F	n/a
Age (yrs)	25(3.6)	24.3 (2.89)	0.793
Height (m)	1.71(0.08)	1.75(0.075)	0.909
Mass (kg)	66.9(9.05)	74.71(12.7)	0.096
Right arm span (m)	0.78(0.09)	0.88(0.04)	0.851
Right arm girth (m)	0.29(0.02)	0.30(0.03)	0.956

3.7.2 Kinematics

Table 5 shows the results of the two-way ANOVA analysis on intersegmental angles. Changes in intersegmental angles were significant over the entire time of the climb cycle, except for lumbar flexion/extension, as intersegmental angle changes, particularly thoracohumeral and elbow, were necessary to task completion. Most intersegmental angles were significantly different between groups, though at the shoulder only thoracohumeral elevation was significantly different between groups (Table 5).

Table 5: Results of the joint angle two-way ANOVA analysis showing differences across time, and group and the interaction of both factors. Significant differences at p<0.05 are denoted with an asterisk.

Intersegmental Joint	Rotation	p-value Time	Group	Interaction Time*Group
Elbow	Flexion/Extension	*0.0001	*0.0001	1.000
	Deviation	*0.0001	*0.0001	1.000
	Internal/External Rotation	*0.0001	*0.0001	1.000
Thoracohumeral	Plane of Elevation	*0.0001	0.916	1.000
	Elevation	*0.0001	*0.0001	1.000
	Internal/External Rotation	*0.0001	0.991	1.000
Lumbar	Flexion/Extension	0.872	*0.0001	*0.0001
	Lateral Flexion/Extension	*0.0001	*0.0001	0.808
	Axial Twist	*0.0001	0.734	1.000

The following waveforms show the intersegmental angles throughout the climb cycle and are grouped by segment. Though the differences are subtle, all three elbow angles were significantly different between participant groups (Figure 22). The inexperienced non-climbers were less flexed in support, and more externally rotated throughout support and into early swing (Figure 22). The inexperienced non-climbers had significantly greater thoracohumeral elevation throughout the entire climb cycle (Figure 23). Lumbar flexion was significantly different between participant groups as well, with inexperienced climbers having more extension than the experienced climbers during swing phase only, creating an interaction effect between time and group (Figure 24). The experienced climbers were also in more right lateral flexion than the experienced climbers throughout the entire climb cycle (Figure 24).

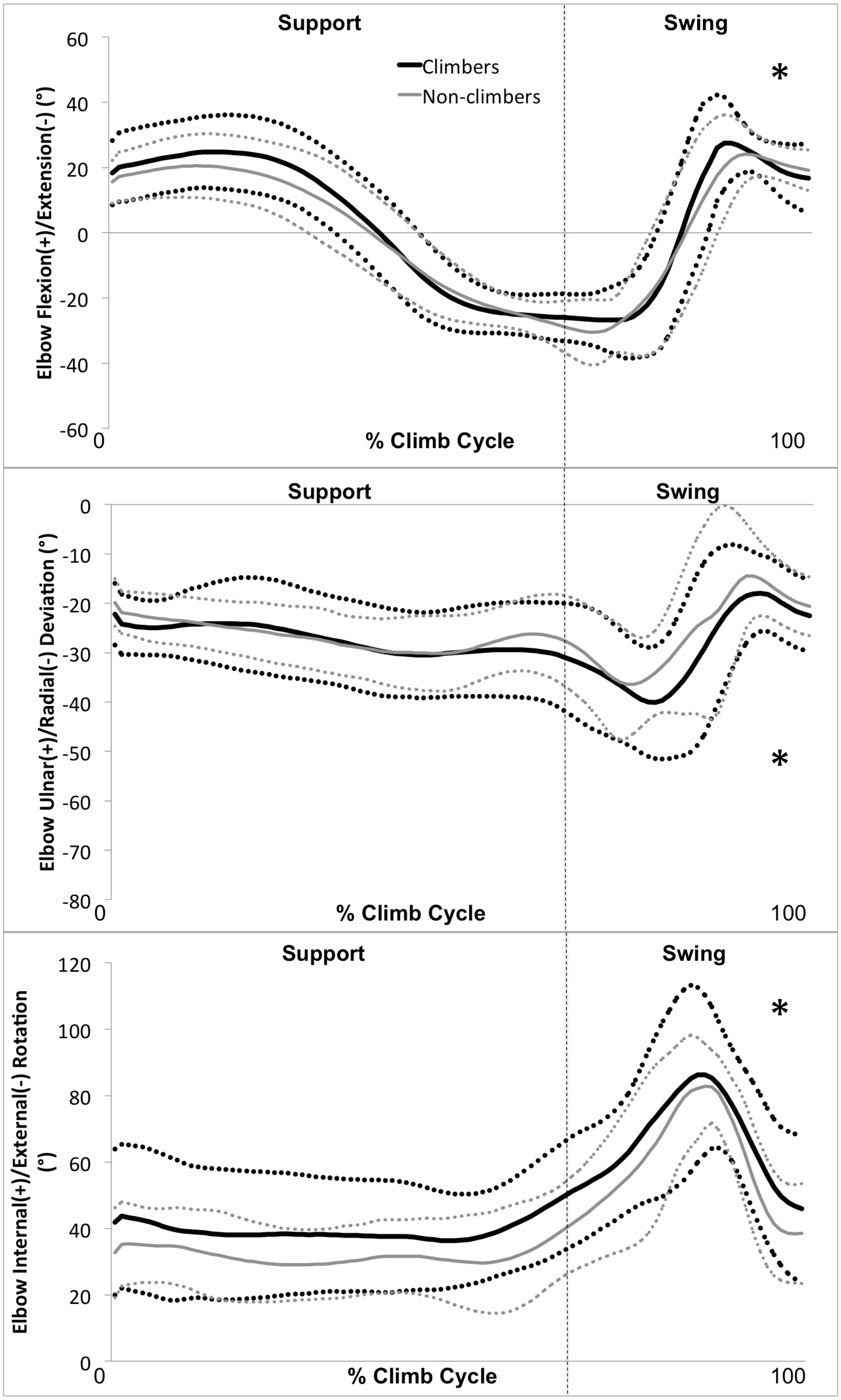


Figure 22: Averaged participant group elbow intersegmental angles for a full right arm climb cycle. Significant cumulative differences in joint angle magnitude throughout the entire climb cycle between participant groups are denoted with an asterisk, *.

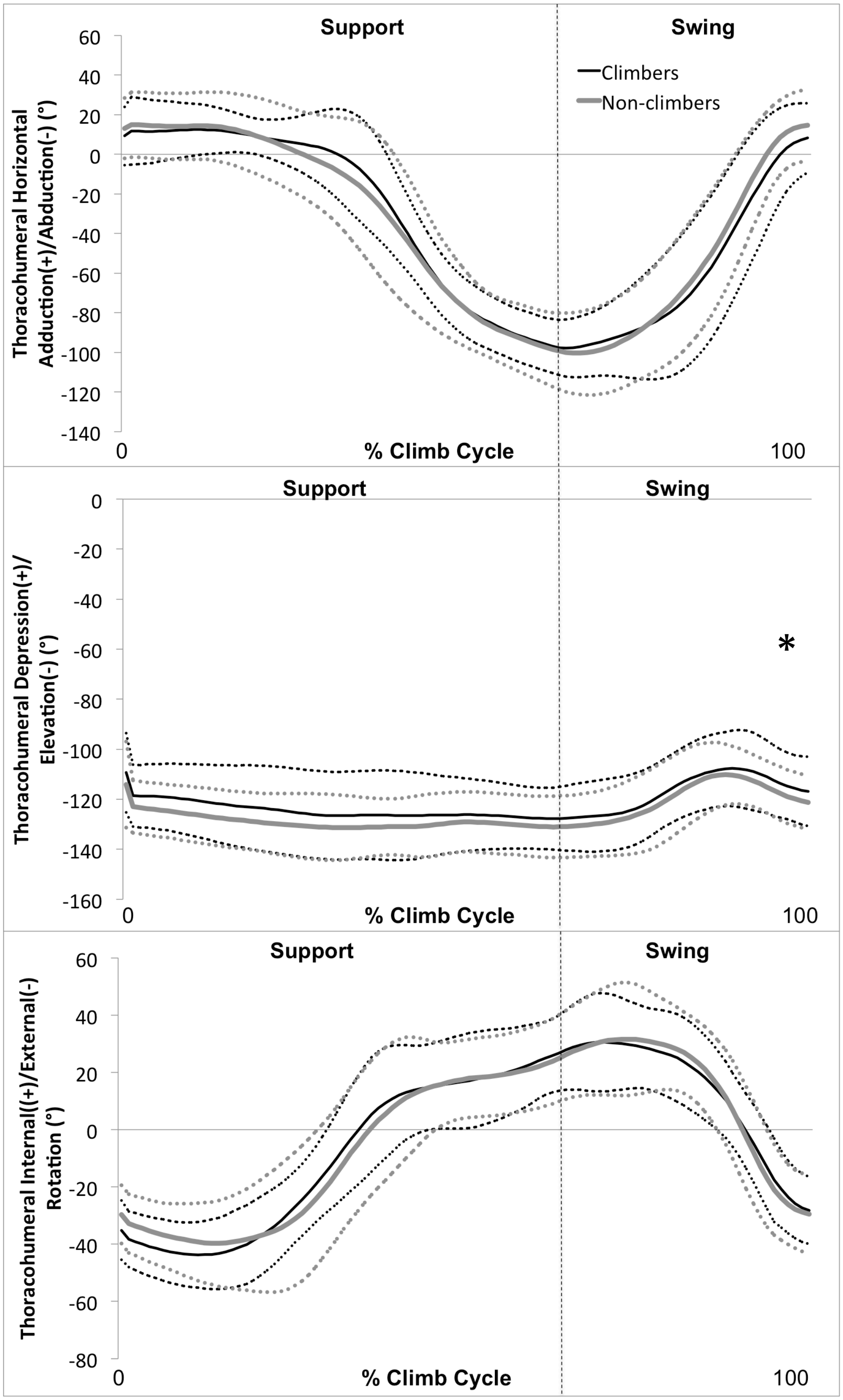


Figure 23: Averaged participant group throacohumeral interesgmental angles for a right arm climb cycle. Significant cumulative differences in joint angle magnitude throughout the entire climb cycle between participant groups are denoted with an asterisk, *.

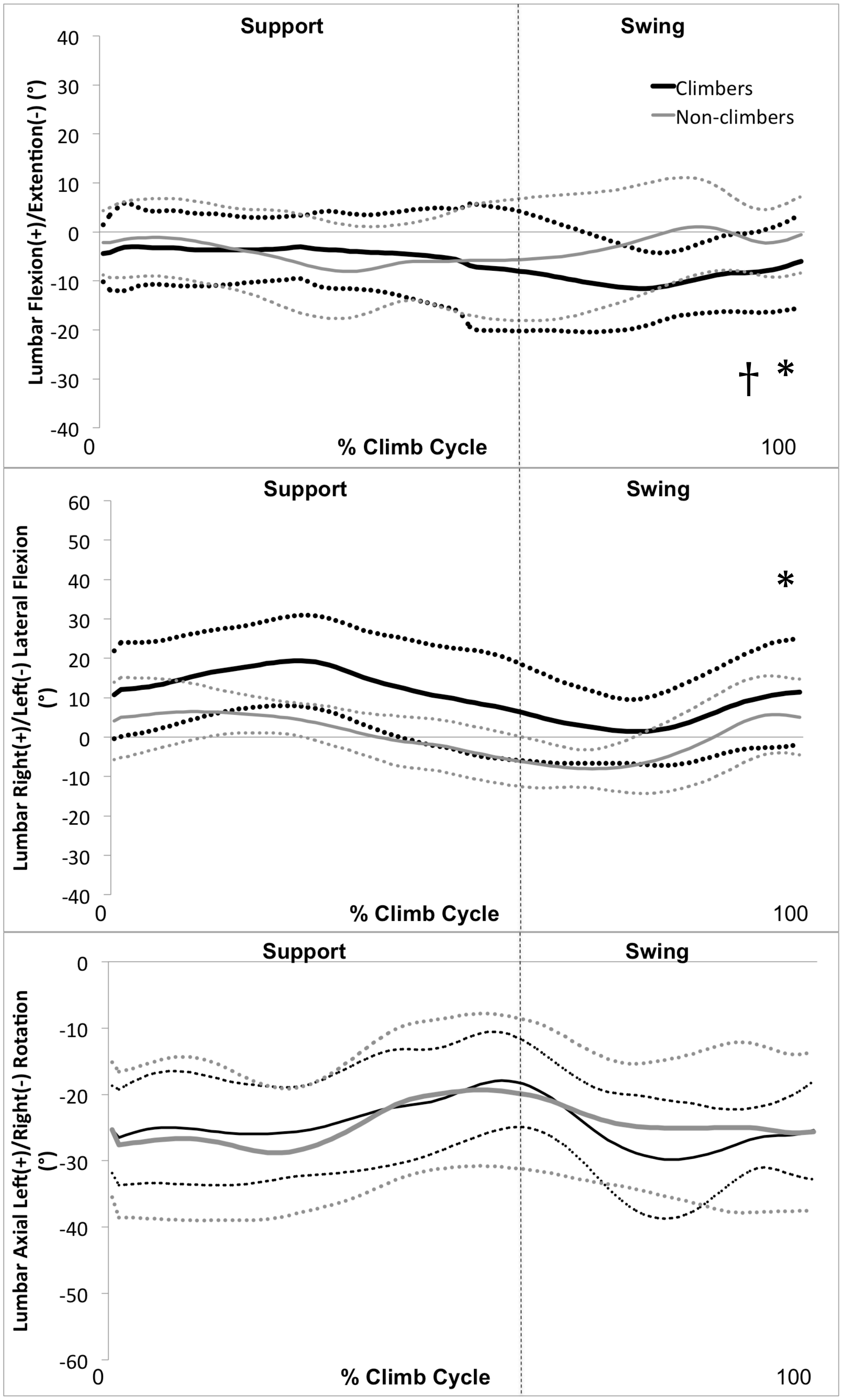


Figure 24: Averaged participant group lumbar intersegmental angles for a full right arm climb cycle. Significant cumulative differences in joint angle magnitudes throughout the entire climb cycle between participant groups are denoted with an asterisk, *. An interaction effect is denoted with an †

3.7.3 EMG

Differences also existed between participant groups in the EMG amplitude (Table 6). All muscles were significantly different across the 100 time points of the climb cycle, as the activation levels of all muscles changed widely throughout the cycle. Half of the muscles were significantly different between participant groups in muscle activation amplitude (Table 6). The anterior deltoid had a significant interaction effect, as the EMG amplitude differences between the two participant groups changed over the climb cycle.

Table 6: P-values from the two-way ANOVA, showing significant differences in muscle activation level between participant groups for each muscle. Significant differences are denoted with an asterisk at $p<0.05$, and represent differences over the whole climb cycle, not a specific time point.

	p-value		
Muscle	**Time**	**Group**	**Interaction Time*Group**
Anterior Deltoid	*0.0001	*0.0001	*0.016
Posterior Deltoid	*0.0001	0.342	1.000
Biceps Brachii	*0.0001	*0.0001	1.000
Triceps Brachii	*0.0001	0.319	1.000
Infraspinatus	*0.0001	*0.0001	0.661
Supraspinatus	*0.0001	0.492	0.986
Pec Major (Clav)	*0.0001	0.464	1.000
Pec Major (Stern)	*0.0001	*0.0001	1.000
Upper Trap	*0.0001	0.664	0.998
Middle Trap	*0.0001	*0.0001	0.594
Latissimus Dorsi	*0.0001	0.885	1.000
Serratus Anterior	*0.0001	*0.0001	0.917

The differences in Table 6 are visualized in muscle waveforms in the following series of figures. Mean waveforms for each group are shown, along with dotted lines representing a single standard deviation. Each figure pairs two muscles together from the same muscle group or body region.

The anterior deltoid had two phases of high activity, once in support and once in swing phase. The posterior deltoid was most active in late swing (Figure 25). The anterior deltoid was activated at a higher amplitude by the non-climbers (Figure 25).

The group differences in the anterior deltoid only existed at the end of support phase, and into swing phase (Figure 25).

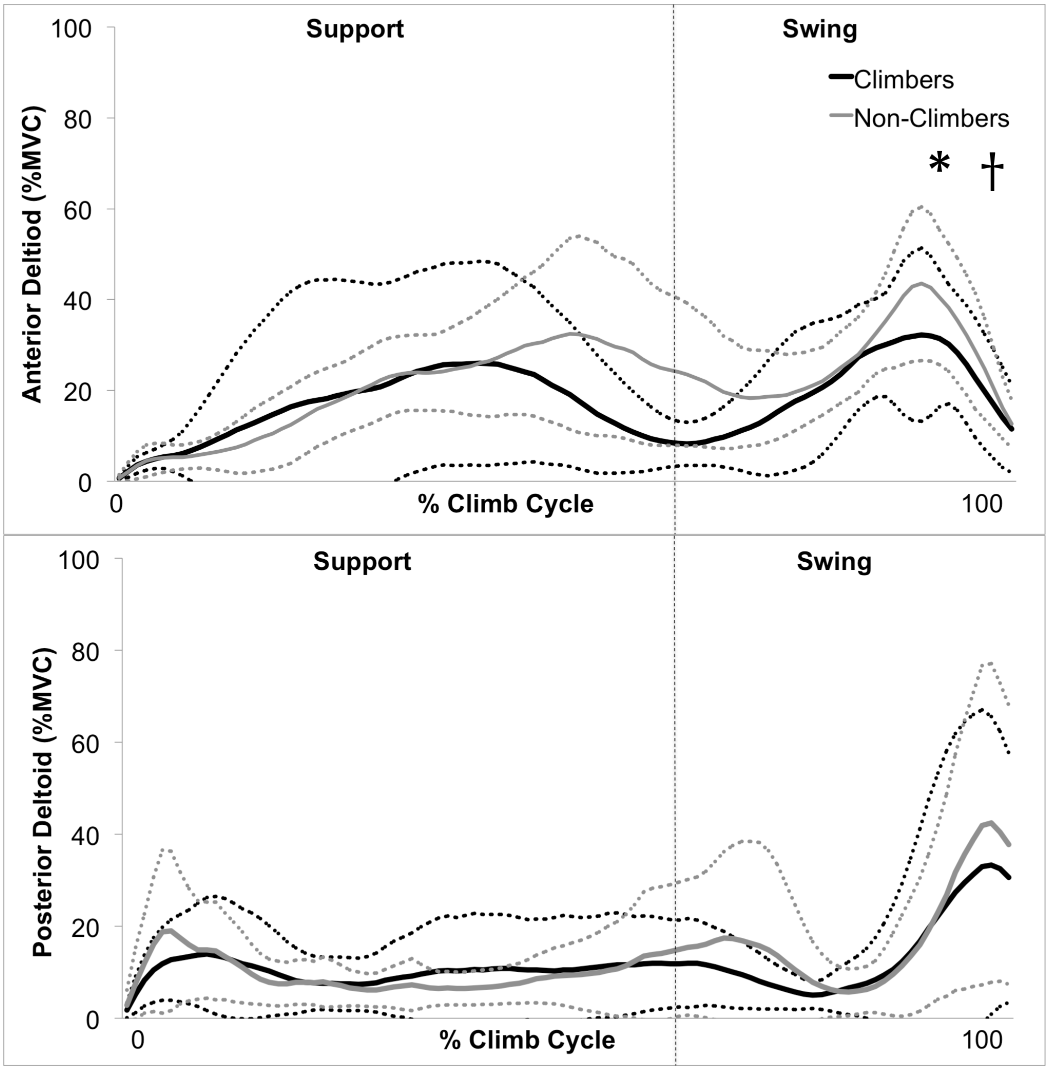


Figure 25: The normalized muscle activity of the anterior and posterior deltoids in the two participant groups for a full right arm climb cycle. Significant differences in EMG amplitude accumulated throughout the entire climb cycle between participant groups are denoted with an asterisk, *. A significant interaction between time and group differences in amplitude is denoted with †.

The biceps brachii was highly active in support phase, while the triceps brachii was most active in late swing into early support phase (Figure 26). Inexperienced non-climbers activated the biceps brachii at a higher percentage of maximum throughout the entire climb cycle, with activation nearing or exceeding MVE (Figure 26). There was also a large variability of muscle activation in both participant groups (Figure 26).

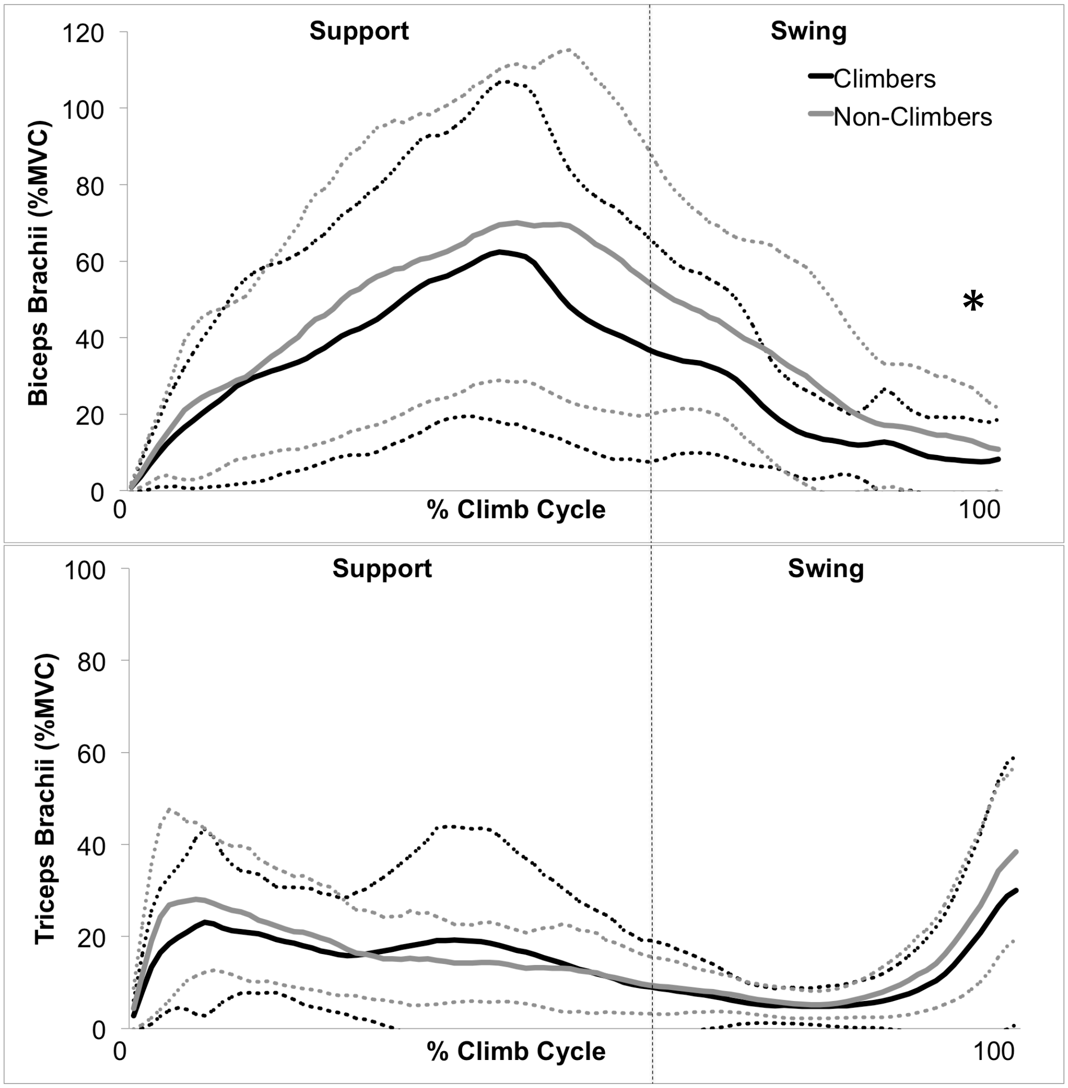


Figure 26: The normalized muscle activity of the biceps brachii and triceps brachii in the two participant groups for a full right arm climb cycle. Significant differences accumulated throughout the entire climb cycle between participant groups in EMG amplitude are denoted with an asterisk, *.

Supraspinatus and infrapsinatus were active in both phases of climbing, but were most active in swing phase (Figure 27). Inexperienced non-climbers also activated infraspinatus at a higher amplitude, particularly during the transition from support to swing, and in late swing (Figure 27). The upper standard deviation band indicated that many participants exceeded their MVE in swing phase (Figure 27).

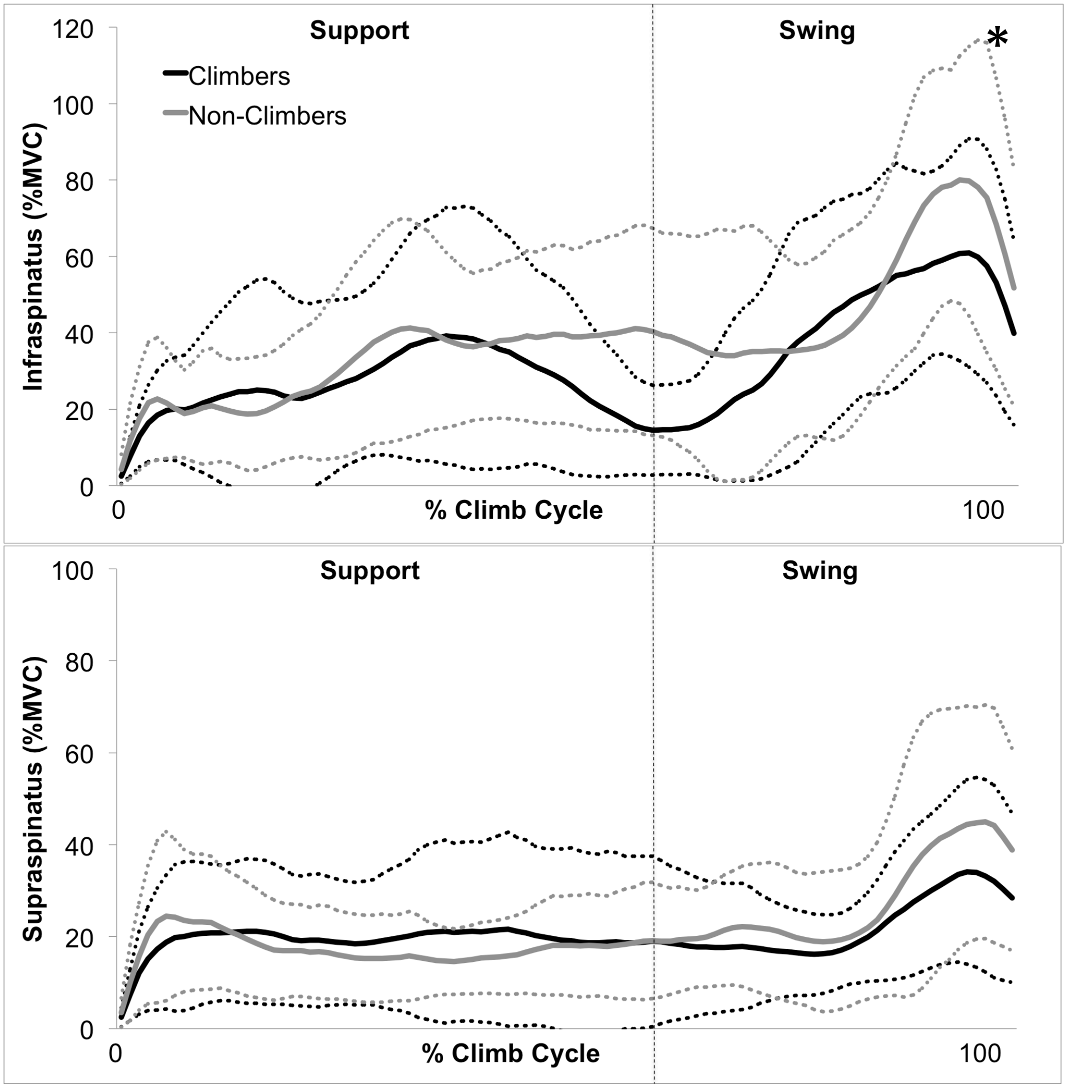


Figure 27: The normalized muscle activity of the infraspinatus and supraspinatus in the two participant groups for a full right arm climb cycle. Significant differences accumulated throughout the entire climb cycle between participant groups are denoted with an asterisk, *.

The pectoralis major was active in support phase, but only the sternal head had high activity in swing phase. The pectoralis major sternal head was activated at a higher amplitude by the inexperienced non-climbers throughout the entire climb cycle (Figure 28). This difference between groups was more pronounced in the support phase. There was a stark difference in the activation level of the two heads of the pectoralis major, as the sternal head was well above maximum voluntary isometric contraction (Figure 28). Both muscles were active in support phase, but the clavicular head was much quieter in swing phase (Figure 28).

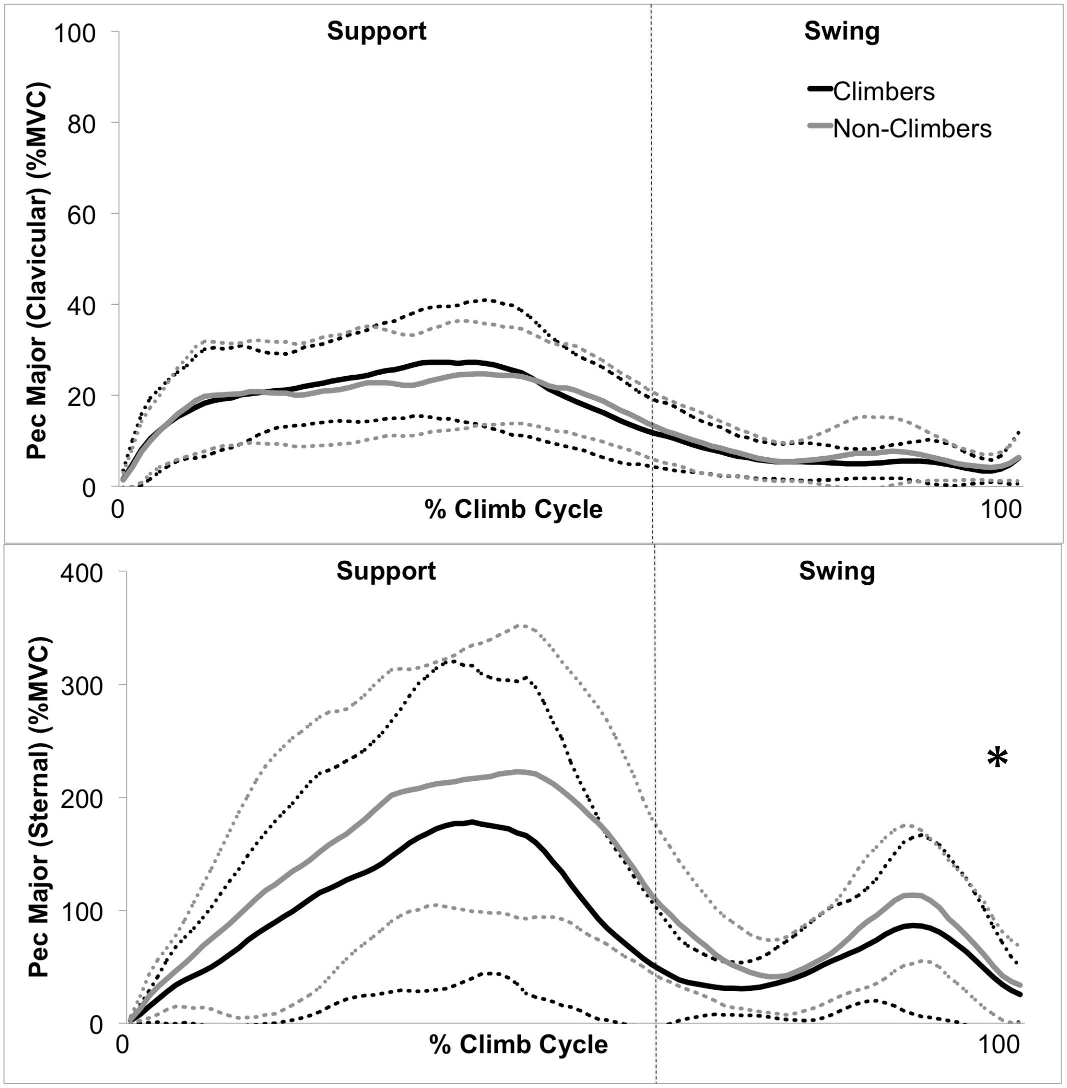


Figure 28: The normalized muscle activity of the pectoralis major clavicular and sternal head in the two participant groups for a full right arm climb cycle. Significant differences accumulated throughout the entire climb cycle between participant groups are denoted with an asterisk, *.

The upper trapezius had a burst of activity in both phases of the climb cycle. Middle trapezius increased activity in support phase and into swing phase, but reduced greatly by mid-swing. The inexperienced non-climbers activated the middle trapezius more during late support and early swing phase (Figure 29). There was a similar trend in the upper trapezius, but the difference between groups was not statistically significant. While the middle trapezius mostly contributed to support phase, the upper trapezius contributed greatly to both phases.

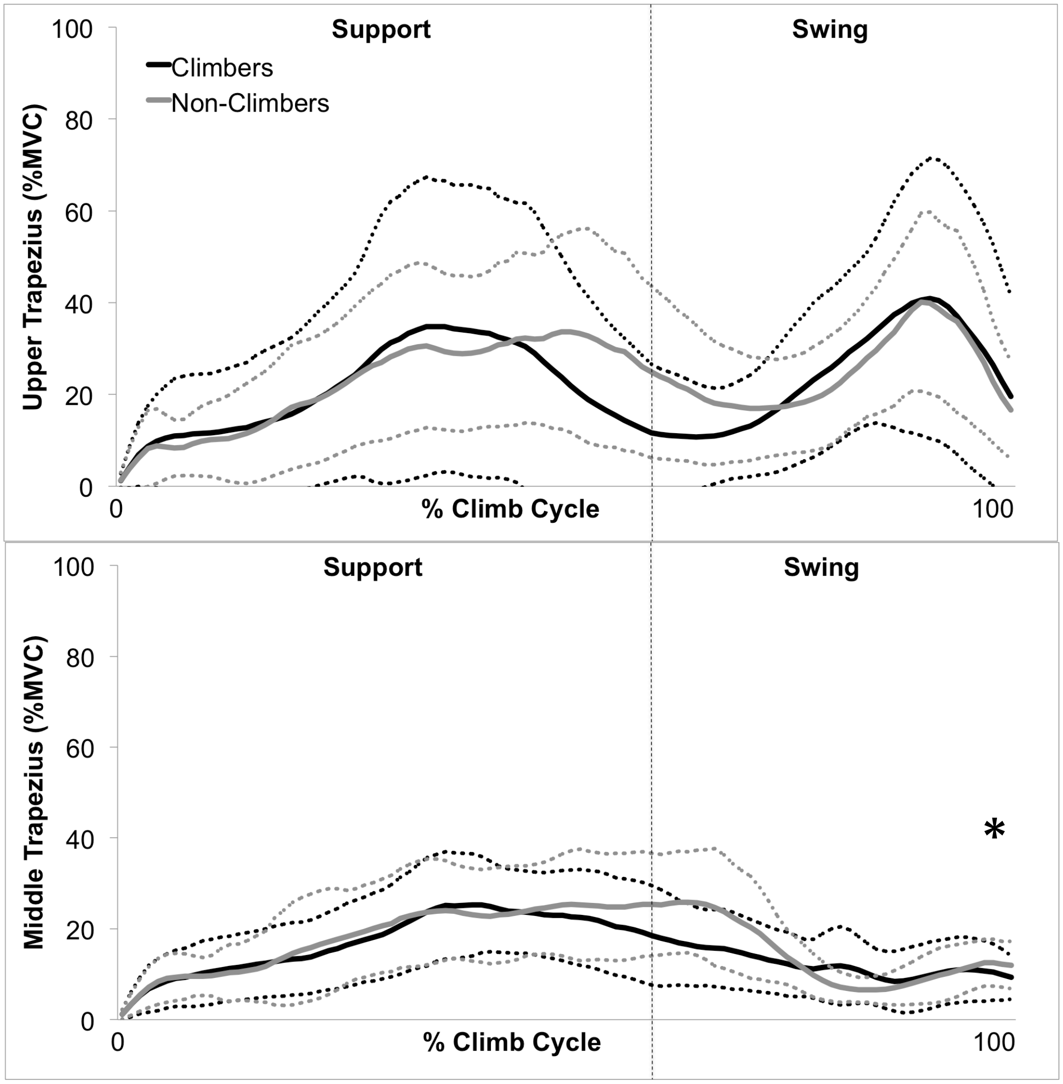


Figure 29: The normalized muscle activity of the upper and middle trapezius in the two participant groups for a full right arm climb cycle. Significant differences accumulated throughout the entire climb cycle between participant groups are denoted with an asterisk, *.

The latissimus dorsi was mostly active in support phase (Figure 30). Serratus anterior was active in support phase, and increased activity even more into swing phase. By late swing phase, serratus anterior was activated at nearly MVE or higher. The experienced climbers activated serratus anterior at a significantly higher amplitude in swing phase (Figure 30).

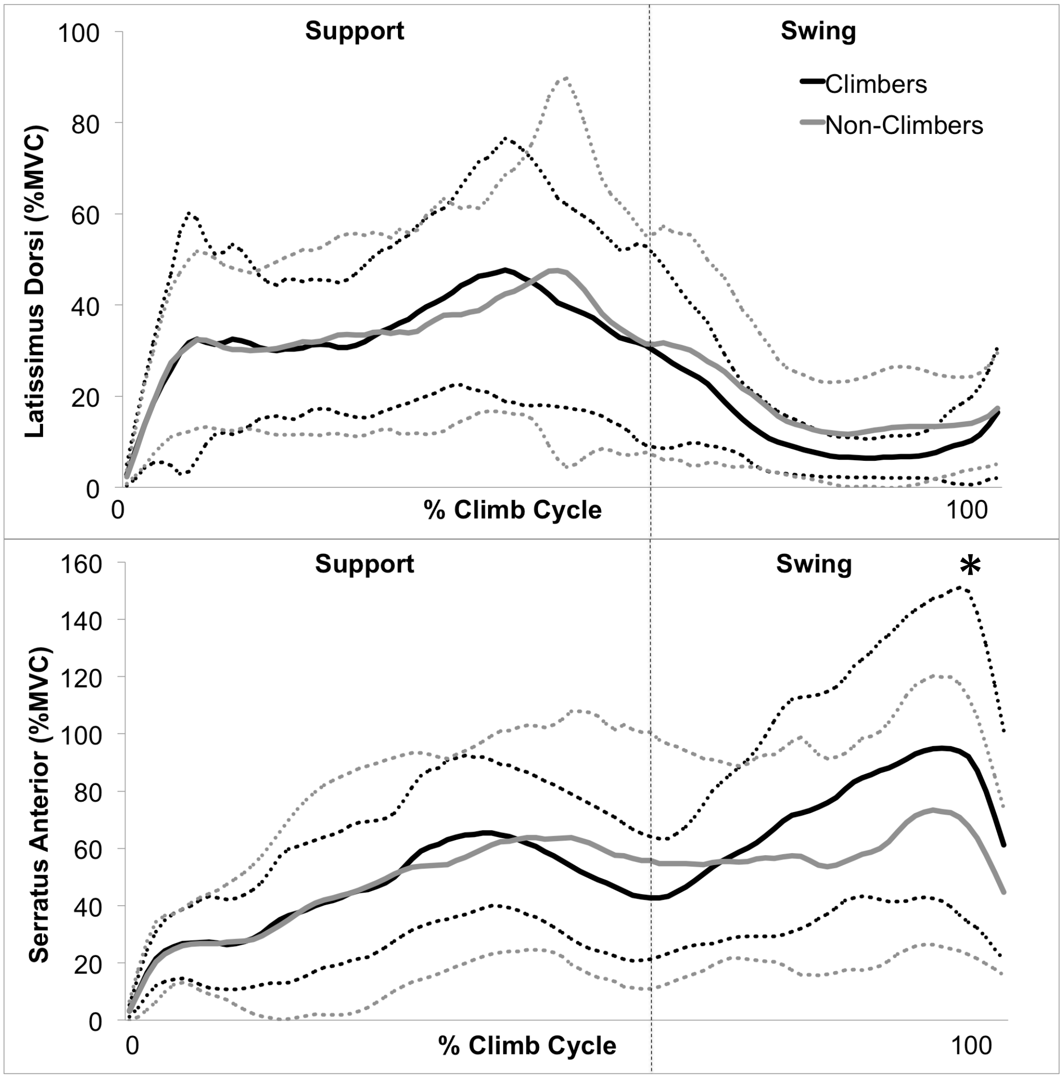


Figure 30: The normalized muscle activity of the latissimus dorsi and serratus anterior in the two participant groups for a full right arm climb cycle. Significant differences accumulated throughout the entire climb cycle between participant groups are denoted with an asterisk, *.

3.7.4 Between Species Comparisons

A comparison between chimpanzees and humans was conducted for both kinematics and muscle activity. Two-dimensional elbow and thoracohumeral angle were measured from videos of humans and chimpanzees performing horizontal bimaual arm-suspension climbing. The resulting elbow and thoracohumeral angles represent a mostly sagittal plane flexion/extension and arm elevation, respectively. The chimpanzee angles fell within the boundaries of the 95% confidence interval of the human angles (Figure 31). The results of this analysis indicated no notable functional, population-level differences between the chimpanzee and experienced climber human sample in two-dimensional elbow or thoracohumeral angles. There was a small portion of the chimpanzee waveform that was outside the lower bound of the human 95% confidence interval (Figure 31). This portion was small enough to be approximated as less than or equal to the 5% that would be predicted to fall outside the confidence interval.

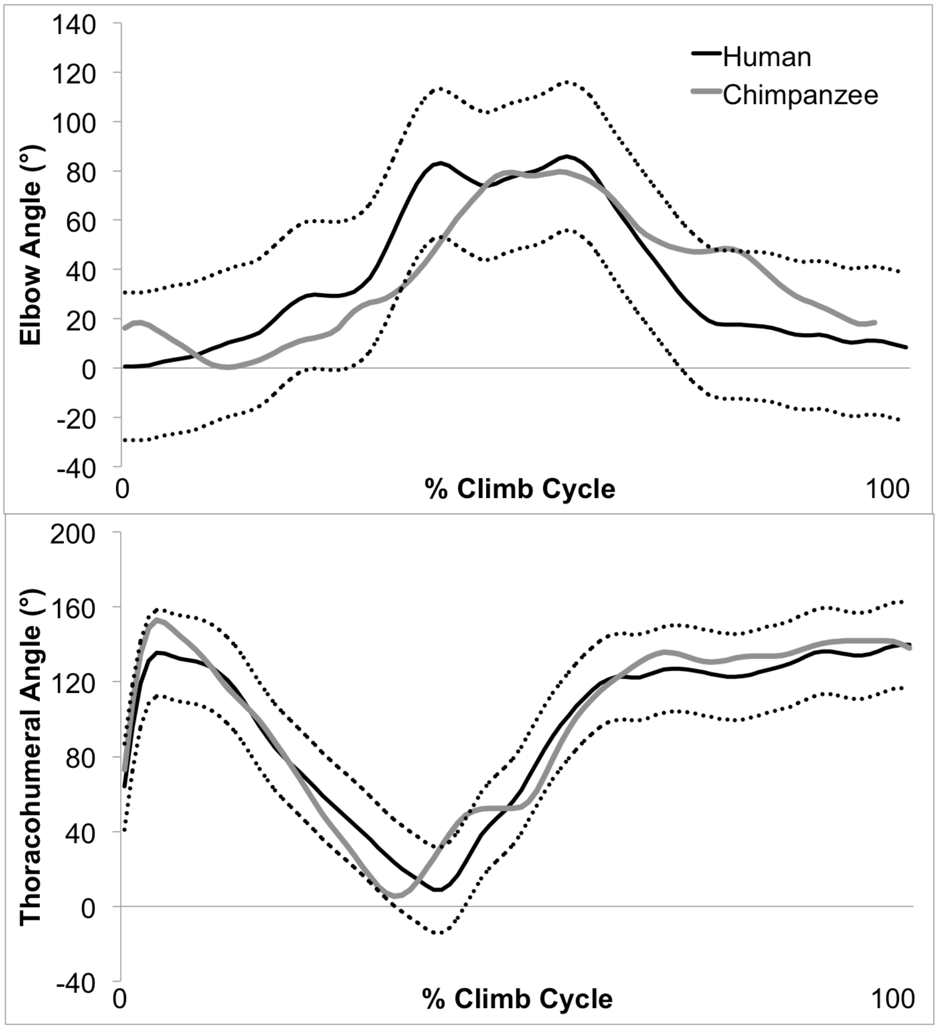


Figure 31: Comparison of chimpanzee joint angles to the human joint angles. The dotted line represents the 95% percent confidence interval.

To conduct a visual muscular activity comparison between chimpanzees and humans, the human EMG data in the present study was modified to be visually similar in presentation to chimpanzee data published by Larson and colleagues (1986, 1991). The standard deviation lines were removed from the Figures 25-30, leaving only the mean waveforms for both human participant groups, and the area under the curve was greyed. The duration of the support and swing phases were left as they were recorded, with support phase consisting of a larger proportion of the climb cycle.

Chimpanzee EMG waveform images were pulled directly from publications (Larson et al., 1986, 1991). The chimpanzee data reported was typically collected from only one or two subjects and normalized to the highest recorded RMS or highest recorded value during the task (Larson et al., 1986, 1991). The presentation of the chimpanzee data standardizes the support phase and swing phase time into equal duration parts of the climb cycle, separated by a dashed line. The dark areas of the chimpanzee figures represent activity that consistently occurs in at least two-thirds of the recordings of the subject(s) recorded. The hatched areas represent the less consistent activity that occurred between one-third and two-thirds of the time (Larson & Stern Jr, 1986).

The visual analysis of the muscle activations showed numerous similarities between species in the timing of muscle activation. The experienced climbers often had more distinct bursts of phasic activity than the inexperienced non-climbers, particularly in anterior deltoid, infraspinatus, upper trapezius and serratus anterior (Figure 32). These more obvious phasic changes in experienced climbers were more consistent with chimpanzees, who also had distinct, phasic bursts of activity. The most glaring species difference existed in the posterior deltoid. Chimpanzees activated this muscle in mid- to late-support, and into early swing. Humans activated this muscle during those phases, but had the most marked activation in late swing (Figure 32). As the human EMG was normalized to MVE and the chimpanzee data normalized to a submaximal highest recorded value during the task, the amplitudes recorded in Figure 32 can be presumed to represent proportionately higher muscle activity in humans than chimpanzees.

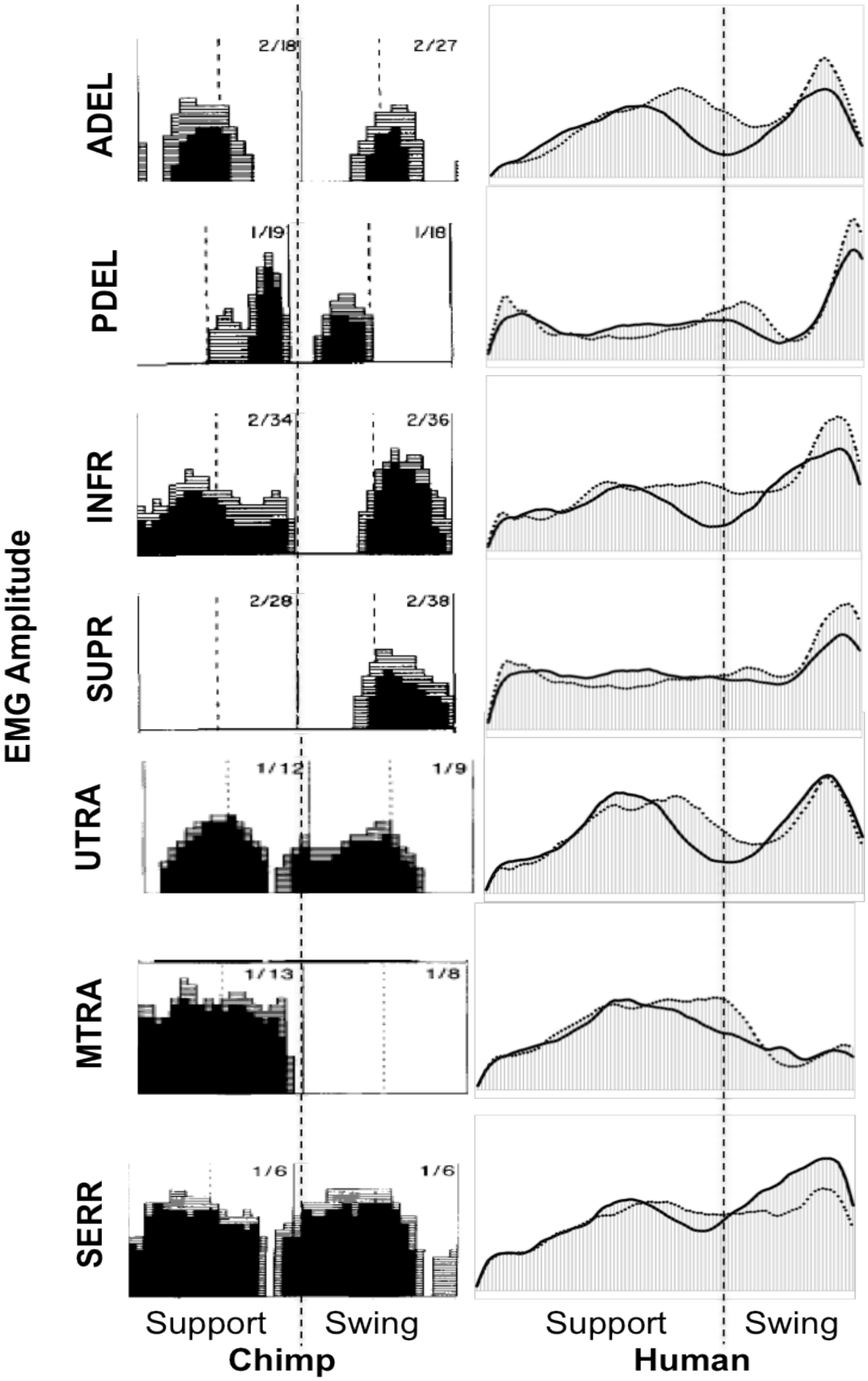


Figure 32: Comparison of chimpanzee and human muscular action while climbing across a set of horizontal rungs. The black solid and grey dotted human lines represent averaged experienced climber and inexperienced non-climber humans, respectively. Due to different EMG measurement and processing techniques, the y-axis represents a qualitative EMG amplitude comparison between chimpanzees and humans. The support and swing phase are distinguished for both species.

3.8 Discussion

This study represents the first rigorous attempt to characterize human horizontal bimanual climbing ability with advanced biomechanical methods, and make cross-species comparisons with nonhuman primates that habitually climb. Similarities existed between human participant groups, and also between species in both kinematic strategies and muscle activation patterns. However, inexperienced non-climber humans typically activated the musculature surrounding the shoulder at a significantly higher relative amplitude than experienced climbers. Kinematic differences occurred at all three intersegmental joints between human participant groups. While the qualitative analysis between species showed similar joint angles between an experienced human climber and a chimpanzee, humans activated their posterior deltoid much differently than chimpanzees.

Hypothesis one was supported, as the inexperienced non-climbers used different kinematic strategies that included more thoracohumeral elevation and less flexion.

Hypothesis two was mostly supported. For a large percentage of the climb cycle, both participant groups sustained mean activity of the measured muscles above 25% MVE, with peak values that neared or exceeded 100% MVE. The exception was posterior deltoid and middle trapezius. Both these muscles had relatively lower activations around 10-20% for most of the climb cycle.

Hypothesis three was also supported. With the exception of the serratus anterior, inexperienced climbers activated their muscles at a higher proportion of MVE than the experienced climbers.

Hypothesis four was supported. The two-dimensional joint angles derived from video approximately matched between the humans and chimpanzees.

Hypothesis five was mostly supported. Humans had similar timing of muscle activity bursts as chimpanzees, with the notable exception of posterior deltoid. Experienced climbers had more obvious phasic changes that mimicked chimpanzees than the inexperienced non-climbers.

3.8.1 Kinematic Climbing Strategies

Kinematics and muscle activation patterns followed predictable phasic changes in the climb cycle. The most notable changes in amplitude generally coincided with the shift from right arm support to right arm swing.

3.8.1.1 Kinematic Climbing Strategies

Though the differences between participant groups in arm motion were small, they represent different functional strategies that likely affected the efficiency of the climbing task completion. The inexperienced non-climbers elevated their arm more throughout the entire climb cycle, and flexed their elbow less in support and mid-swing. Brachiating primates often flex their elbow in mid and late support phase to raise the body, shift the torso toward the trailing support limb and create potential energy for use during swing phase (Larson & Stern Jr, 1986; Larson & Stern, 2013). The experienced climbers may have had less arm elevation and more elbow flexion to also elevate their body and improve their reach range by positioning the body more forward in the direction of motion. This could indicate more muscular ability in experienced climbers to enable pulling themselves up and improving their reach position for swing phase, or a method to increase forward momentum, or both. The greater arm elevation of inexperienced non-climbers placed the center of mass closer to the support rung, providing greater stability (Larson & Stern Jr, 1986). However, this likely incurred the cost of reducing arm reach and momentum (Larson & Stern Jr, 1986).

The axial motion of the elbow in both participant groups aided the performance of the climbing task by contributing to forward rotation and movement of the body and swinging arm. The elbow was more internally rotated in the experienced climbers. During support phase – particularly during contralateral arm swing – internal rotation pronates the forearm (An et al., 1984). This axial rotation is extremely important in climbing behaviors, with a particularly special combination of large range of motion, strength and stability existing in hominoid forearms (Sarmiento, 1987, 1988; Stern & Larson, 2001). Internal rotation at the elbow is a mechanism to rotate the body in the direction of the contralateral arm swing, particularly in overhead hanging and swing postures (Larson & Stern, 2013; Sarmiento 1987, 1988). Internal rotation was another kinematic strategy used by the experienced climbers to improve body position during climbing, improving task efficiency. Less internal rotation in the inexperienced climbers may have been a consequence of the kinetic chain throughout the upper extremity (Larson & Stern, 1986), or muscular deficits. Humans have well-documented proportionately smaller upper extremity muscle mass (Walker, 2009). This is particularly pronounced in the forearm, where a tradeoff of less power for more fine motor control exists (Walker, 2009; Zihlman, 1992). Less developed forearm musculature due to less climbing experience in inexperienced non-climbers may have prevented achievement of more efficient kinematic strategies.

The observed, group-specific, motions of the lumbar spine were likely kinematic strategies to enhance forward momentum of the body. There was limited range of motion for rotations about the lumbar spine. This was expected, as the torso remains fairly upright, and along with the lower extremity contributes to the mass on the end of the pendular arms of the upper extremity (Larson, 1988; Usherwood et al., 2003). However, the torso and lower extremity mass is utilized in brachiation for mechanical purposes. Primates often create lateral flexion in the contralateral direction of arm swing to create energy and forward momentum for each swing (Larson et al., 1991; Larson & Stern Jr, 1986). Lumbar extension in swing is also common in primates (Fleagle, 1977). This motion elevates the mass of the lower extremity and torso, creating more potential energy to be converted into kinetic energy when the body swings forward, and can conserve potential energy for the subsequent climb cycle (Fleagle, 1977; Larson et al., 1991). The right lateral flexion and axial rotation of the experienced climbers during right arm support and left arm swing raised the center of gravity and shifted it away from the left arm swing. At the commencement of left arm swing, a greater “drop” in center of gravity and increased acceleration in the forward direction is created, fueling the forward motion of swing phase (Larson & Stern Jr, 1986). For the inexperienced non-climbers, greater lumbar extension in swing created energy to produce forward motion toward the next subsequent rung (Fleagle, 1977). Though the difference between groups was small, the greater right lateral flexion in experienced climbers and extension in inexperienced non-climbers could represent separate strategies for producing forward momentum in each group. That neither climbing group performed lumbar extension and lateral flexion concurrently may have been due to limited need for increased forward momentum to perform the present, self-paced climbing task.

3.8.1.2 Muscular Climbing Strategies

The greatest muscular contributors to support phase were biceps brachii, anterior deltoid, latissimus dorsi, serratus anterior, upper and middle trapezius, and both heads of the pectoralis major. The climbing task required support of the full body mass through the right arm in single support phase during left arm swing, and half of the body mass during double support phases. This required large muscle forces to counter traction at the upper extremity joints, and the moments created about the joints (Larson et al., 1991; Usherwood et al., 2003). Of the muscles recorded in this study, those active in support represented some of the largest upper extremity and torso muscles, capable of producing large muscle forces to stabilize the elbow and shoulder (Inman et al., 1944). Glenohumeral stabilizers such as infraspinatus and anterior deltoid were very active, ensuring the glenohumeral joint reaction force was directed into the glenoid cavity. Scapular stabilizers such as latissimus dorsi and serratus anterior were also highly active, controlling rotation of the scapula. Pectoralis major controlled internal rotation of the arm through support phase as the body rotated forward (Larson & Stern, 1986). The middle trapezius prevented superior translation of the scapula, while the upper trapezius likely controlled head rotation as the eyes followed left and right arm motion (Larson et al., 1991). These muscles would have also helped to maintain elevation and horizontal abduction of the glenohumeral joint in a position to improve reach range (Larson & Stern Jr, 1986). The biceps brachii activation was necessary to create an elbow flexion moment, as elbow flexion elevates the body and creates potential energy for swing phase (Larson & Stern Jr, 1986; Larson & Stern, 2013).

Swing phase was characterized by activity from most of the muscles recorded, with greater spikes of activity in later stages of swing phase. This included the triceps brachii, anterior and posterior deltoids, infraspinatus, supraspinatus, serratus anterior, upper trapezius and pectoralis major sternal head. The majority of these muscles were most active from mid to terminal swing. Mid to late swing is when the arm swings forward and elevates again to reach the next support rung (Larson et al., 1991). This phase of swing requires more muscle action to counter gravitational pull. In this phase of the climb cycle, these muscles act to control lateral rotation and protraction of the scapula, elevation and horizontal adduction of the humerus, and extension of the elbow (Larson et al., 1991; Larson & Stern Jr, 1986). The serratus anterior was active throughout the entire swing phase. The serratus anterior is recruited to not only produce scapular rotation in early swing as the arm lowers and horizontally abducts even more, but to stabilize the descent of the scapula and thorax as the propulsive forward motion of the body brings the hand toward a support rung (Larson et al., 1991).

There were different muscle strategies between participant groups, as statistically significant differences between groups occurred in the anterior deltoid, biceps, pectoralis major (sternal head), infraspinatus, serratus anterior, and middle trapezius. These differences existed throughout the entire climb cycle in the biceps brachii and pectoralis major sternal head. In the other muscles, differences were most pronounced at the support-to-swing exchange. The experienced climbers more often decreased muscle activation in terminal support and early swing phase. Early swing is the least taxing point of a climb cycle, as arm elevation reduces, and the potential energy from the support phase kinematics begins forward motion (Usherwood et al., 2003). This represented a transient opportunity for a brief muscle activity reduction. The increased muscle activity in inexperienced climbers likely improved stability around joints through antagonistic pairing (Lugo et al., 2008; Veeger & van der Helm, 2007). Owing to their lack of climbing experience, increased muscle activity was a potential strategy to improve joint stability, compensating for lower task skill level and confidence.

Though the inexperienced non-climbers generally had higher muscle activity, experienced climbers activated serratus anterior more in swing phase. The serratus anterior is a scapular stabilizer and protractor, which is important during the swing forward of the right arm in swing phase (Larson et al., 1991). Climbing requires strong stabilization of the scapula in support phase to prevent superior movement of the bone relative to the torso, and in swing phase to raise the arm through scapular rotation to make support rung contact (Larson et al., 1991). The serratus anterior is a very large muscle in brachiating primates, and one of the most important contributors to scapular rotation and stabilization (Larson et al., 1991; Jenkins et al., 1978; Stern et al., 1980). The lower activation in inexperienced climbers implies that scapular control was achieved via greater use of other synergistic muscles, such as the trapezius. That the experienced climbers activated this muscle more may be an indication of a training effect that leads to adopting muscle activation patterns that mimic those of habitual locomotor climbing species. Experienced rock climbers have less static scapular lateral rotation than individuals without rock climbing experience for the same arm elevation (Roseborrough & Lebec, 2007). The reason for this is unknown, but is hypothesized to relate to muscular adaptations placing greater demands on the serratus anterior (Roseborrough & Lebec, 2007). Several muscles were active beyond maximum voluntary isometric exertion during the horizontal climbing task. Although activation was high in most muscles, it was exceptionally high in pectoralis major sternal head, biceps brachii, latissimus dorsi, and serratus anterior. This amplitude highlights the difficulty of climbing, and the taxing nature of upper extremity locomotion for modern humans. It was also rare that any recorded activity values were below 20% MVE throughout the climb cycle. Rock climbers have a 75-90% upper extremity injury rate due to overuse (Wright et al., 2001). More than 30% of recreational rock climbers are reported to have rotator cuff tendonitis or impingement (Rooks, 1997). The high muscle activation amplitudes during the present climbing study support previous work indicating that climbing is physically demanding, and associated with a high risk for muscle fatigue-related joint injuries (Lewis et al., 2001: Roseborrough & Lebec, 2007). It is unlikely that the workload from the upper extremity musculature necessary to complete the climbing task, even in the experienced climbers, is sustainable over extended periods of time without early onset of fatigue and fatigue-related dyskinesis (Chopp et al., 2010; Cote & Bement, 2010).

3.8.1.3 Between Group Variability

Large variability was noted in both participant groups kinematics. While both participant groups had mean intersegmental angle waveforms with similar trajectories, the variability indicates a variety of kinematic strategies were employed by individual participants. Overall movement strategies often had similar outcomes, such as elbow extension and horizontal abduction into late support and early swing phase. These types of motions were necessary consequences of forward progression of the body during a climb cycle, as the right arm moved behind the body after the left arm swung forward to subsequent rung contact (Larson et al., 1991). However, the combinations of intersegmental motions used by each participant were inconsistent. In particular, those movement strategies which may have improved climbing efficiency were highly variable. As an example, the combination of elbow flexion and axial rotation to improve reach range toward the next rung was variable between participants. In both groups, some axially rotated more to rotate the body toward the next rung. Others employed more elbow flexion to raise the body closer to the next rung. Other tandem kinematic strategies to improve reach range, such as greater horizontal abduction or lumbar axial rotation to shift the body toward the next forward rung, could also have been utilized. Adoption of inefficient and variable movement strategies, in the acute phase of learning is common (Hashish et al., 2016; Hall et al., 2013). The bimanual climbing task in the present study would have been an unfamiliar task for both participant groups. While the experienced climbers were familiar with climbing activities such as bouldering and rock climbing, these behaviors engage all four extremities and are often vertical ascents and descents (Rooks, 1997). Unfamiliarity with the task likely lead to more variability as participants acquainted themselves with the performance requirements (Tam et al., 2016). Some of the kinematic variability in the present study can likely be attributed to unfamiliarity and even discomfort with the bimanual climbing task.

There was high variability in EMG amplitude of all muscles across participants in both groups, emphasizing the well-known muscular redundancy at the shoulder. Many different muscles can contribute to completing the same arm movement or task (Basmajian, 1967). Participants could use a unique complementary set of muscles to perform the climb cycle. As a result, the activations measured in the present study could vary widely depending on the participant-specific synergistic muscle strategy used to complete the task. Some participants may have opted to rely on fewer, larger muscle groups, whereas others could distribute demands over more muscle groups, reducing the level of activation required of each individual muscle. The variability was generally similar in both participant groups. Therefore, increased skill and familiarity with climbing tasks did not necessarily result in a singular population-level muscular recruitment strategy, possibly indicating anthropometric or other personal influences on technique.

Participants also spanned a wide anthropometric range, which could have affected biomechanical variability. Height, weight and arm span was very different among all participants in both groups. Participants ranged from a 1.5m tall, 46kg mass female to a 1.9m tall, 99kg male. Anthropometric differences affected innate reach range, position of center of mass, and the external force experienced due to gravity for each participant (Winter, 2009). As the rung spacing remained consistent for all participants, each would have required different kinematics to make contact with rung (Thompson et al., 2014). Taller participants with greater arm span would have been able to reach the next rung with less elbow flexion and thoracohumeral depression than shorter participants. Conversely, shorter participants with a smaller arm span would need to employ a combination of kinematic strategies to improve a shorter reach range, such as elbow flexion, thoracohumeral depression and horizontal abduction, and lumbar axial rotation toward the ipsilateral arm (Larson, 1986). Based on anthropometrics, different kinematic requirements to complete the task would have consequently affected the variability in muscular strategies as well (Tam et al., 2016). Greater elbow flexion and thoracohumeral depression in participants with reduced arm span would require greater engagement of muscles such as biceps brachii and latissimus dorsi, respectively. Combined with unfamiliarity with the bimanual climbing task and muscular redundancy, differences in anthropometrics would have greatly affected the kinematic and muscular strategies utilized by each participant.

3.8.2 Comparison to Primate Climbing Strategies

Direct three-dimensional kinematic and muscular activity comparisons were impossible between the human and chimpanzee cohorts, as no three-dimensional kinematics have been reported for chimpanzees and the EMG available utilized different methodologies. The available descriptive data can be used to qualitatively compare the two species to assess general similarities in horizontal bimanual arm suspension brachiation.

3.8.2.1 Between-species Kinematic Comparison

The experienced climber participant group had small kinematic adaptations that were similar to the reported postures of brachiating primates during horizontal bimanual arm suspension climbing. When the two-dimensional chimpanzee kinematics was compared to the population-level distribution of two-dimensional human kinetics, more pronounced functional, population-level similarities emerged between species. Thus, when performing a simple bimanual climbing task, humans can engage in similar kinematic strategies as chimpanzees. As determined by the three-dimensional within-human analysis, with more practice and a more challenging climbing task, these kinematic strategies appear even more similar to primates (Larson & Stern Jr, 1986; Larson et al., 1991). This included postures that use kinematics to improve energetic efficiency and forward momentum, and improve reach range (Larson & Stern Jr, 1986; Larson & Stern Jr, 2006; Usherwood et al., 2003). As chimpanzees and other primates who brachiate as a form of habitual locomotion have efficient kinematics, this result suggests climbing experience in modern humans can lead to moderately more efficient kinematics that are evolutionarily relevant to potential human brachiating ancestry.

Experienced and inexperienced participants in the present study used both pendular and non-pendular swing characteristics, but most participants employed a hybrid approach. Depending on the scenario, chimpanzees engage in both pendular and non-pendular climbing. Pendular climbing uses the torso as a pendulum below the support arm (Larson et al., 1991; Stern et al., 1980). Motion occurs through momentum of the swinging body and arm due to gravity. At terminal swing, the musculature of the shoulder and arm must act to elevate the center of mass and add energy into the pendulum for the next swing cycle (Laron et al., 1991). Non-pendular climbing is a slower paced motion that pivots the body through axial rotation of the arm and forearm. The arm remains more straight and elevated through support phase, and remains elevated in swing phase (Larson et al., 1991). Evidence of pendular swing behavior of adding energy back into the pendulum through muscle action appears in the terminal swing muscle activity (Figures 25 – 30). The kinematic strategies of the experienced climber group may also be indicative of more pendular elements integrated into their climb cycle (Larson et al., 1991; Larson & Stern Jr, 1986). However, all participant groups maintained elevation of the arm above the shoulder in swing phase, and the degree of extension of the lumbar region to achieve pendular motion under the arm was small. Humans have less internal and external rotation range of motion in the upper extremity available than in climbing primates to rotate the body forward using non-pendular techniques (American Academy of Orthopaedic Surgeons, 1965; Larson & Stern Jr, 2006; Usherwood et al., 2003). It is possible that a hybrid approach that introduced some pendular characteristics to an otherwise non-pendular climb cycle was a necessary compensation to increase momentum in the context of limited axial rotation about the arm (Larson & Stern Jr, 1986).

Lack of true pendular swing in humans may have also been a consequence of the task design. The study was designed to be a feasible climbing task for both experienced and inexperienced climbers, resulting in close spacing of the bars on the ladder. Participants were asked to climb at their own self-selected speed and to reach for each subsequent rung during climbing, and not skip rungs to increase difficulty. Following those guidelines, the task rung spacing may have prevented the participants from using a pendular swing, as they were close enough to be reached through non-pendular action. A select group of participants completed some variations on the original task that included skipping rungs, exemplified by the two-dimensional video comparison between species. The comparison of an experienced human climber skipping rungs to a chimpanzee using pendular swing demonstrated large kinematic similarities between species. These similarities included an arc motion of the arm during swing, and more pendular motion of the body mass under the arm. Therefore, under different conditions, humans with dedicated and practiced weight-bearing and climbing use of their upper extremity, are able to achieve similar pendular climbing kinematics of highly specialized brachiators (Chang et al., 2000).

3.8.2.2 Between-species Phasic Muscular Activation Comparison

Human muscle activity was greater than chimpanzees throughout the climb cycle, a consequence of muscular differences between species that affect injury risk. Having a non-weight-bearing upper extremity, humans have an evolved lower proportion of muscle mass in the upper extremity than chimpanzees (Walker, 2009). Humans also have an equal or greater overall body mass than chimpanzees to support during climbing. While humans, chimpanzees and other brachiating primates have less orthopaedic stability at the shoulder than other mammals, the reduced muscle mass to compensate for this low stability in humans, and greater body mass, exacerbates the difficulty of climbing and performing other overhead postures (Codman, 1934; Roberts, 1974). Overhead postures require increased muscular demand in modern humans to stabilize the glenohumeral joint, and often lead to rapid muscle fatigue (Chopp et al., 2010; Ebaugh et al., 2006; McQuade et al., 1998; Tse et al., 2016). Repetitive reaching, forward flexion and elevation tasks performed at 20-25% of MVE lead to task completion failure in less than 30 minutes (Ebaugh et al., 2006; Tse et al., 2016). Performing repetitive maximal force exertions of arm elevation leads to task failure within 2 minutes (McQuade et al., 1998). The lowest activation phases for humans climbing in the present study were generally between 10 and 25% MVE. Therefore, the human risk for fatigue-related injuries are very high in a continuous bimanual climbing task.

Most of the muscles compared between species followed very similar activation timing patterns, except for distinct differences of the posterior deltoid between chimpanzees and humans. The greatest contribution from the posterior deltoid in human climbers occurred during swing phase, particularly terminal swing during upward reach of the arm, with lower activation around 10-15% MVC throughout the support phase. Chimpanzees experienced bursts of activity from posterior deltoid during the second half of support phase and in early swing. Posterior deltoid has been hypothesized to provide propulsive power in the second phase of support phase by elevating the center of mass, as well as possibly resisting tensile stress at the glenohumeral joint (Larson & Stern Jr, 1986). Its activation increases in early arm swing that requires greater propulsive power, such as with the increased distance traveled between support rungs (Larson & Stern Jr, 1986). The lack of true pendular swing in the present human climbers may explain some differences between species in posterior deltoid activation patterns. In non-pendular swing chimpanzees still primarily activate the posterior deltoid in the second phase of support, but its action becomes significantly reduced overall and there is sometimes periodic activity in late swing (Larson & Stern, 1986). The limited propulsive effort required of the present climbing task was a possible cause of the different actions of posterior deltoid between humans and chimpanzees.

Anatomical and muscle architecture differences may also account for differences between human and chimpanzee posterior deltoid activation timing in the climb cycle. While the posterior deltoid performs a propulsive role in chimps, humans are hypothesized to have devolved high force, propulsive mechanisms in the upper extremity (Lewis et al., 2001; Walker, 2009). Chimpanzees have a higher amount of fast-twitch fibers, providing more force and power output for the same amount of muscle tissue (O’Neill et al., 2017). While humans may have once had comparable force capabilities, they are presently more specialized for repetitive, low cost muscle behavior (O'Neill et al., 2017). The human deltoids are also relatively larger than the human rotator cuff, whereas the deltoids are relatively smaller than the rotator cuff in other climbing primates (Santago et al., 2015). This may affect the role of each muscle group in a climbing posture compared to other primates, with the stronger, more fatigue-resistant deltoids being used in a stabilization role in humans while performing difficult tasks such as climbing. Further, the human scapula is less elongated with less superiorly angulated scapular spine, compared to chimpanzees. This results in a more horizontal orientation of the posterior deltoid muscle fibers than in humans (Larson & Stern Jr, 1986). By climbing with a more elevated arm via a hybrid pendular approach, the posterior deltoid in humans may have been oriented better to resist joint traction, and stabilize the glenohumeral joint throughout support phase than contribute propulsive power.

3.8.3 Overall Climbing and Overhead Strategies

While experienced climbers employed more efficient muscular strategies, all participants demonstrated muscular activity levels that would likely induce fatigue and musculoskeletal injuries. Differences between the two participant groups showed that the inexperienced non-climbers had greater activation from a number of muscles, and less activity reduction during phasic changes. Inexperienced climbers may have prioritized increased joint stabilization over efficiency, joint flexibility and reach range. Greater agonist-antagonist muscular activation pairing through the climb cycle, particularly at phasic changes where experienced climbers reduced activation, while less efficient, would increase joint stabilization (Veeger & van der Helm, 2007). Experience with climbing was associated with beneficial changes to muscular activity, making small adaptations that mirror primates that habitually climb. However, the activity level required from the upper extremity musculature in both participant groups was still extremely high. Sustained and repetitive elevated arm tasks above 10% of MVE cause muscle fatigue (Jonsson, 1988). As muscle activity during the climbing task averaged above 25% throughout the climb cycle, muscular fatigue and associated injuries are highly likely during climbing tasks. This highlights the differences in muscular volume between modern humans and brachiating primates, as humans have evolved to have a non-weight-bearing upper extremity adapted to habitually lower external loads (Lewis et al., 2001).

The climb cycle was comprised of a large range of shoulder motion, including overhead postures, which are particularly challenging in modern humans. The more flexed elbow, less elevated arm, greater lateral lumbar flexion of the experienced climbers served to raise the center of gravity and orient the torso more backward, inducing a greater acceleration when forward motion occurred (Larson & Stern Jr, 1986). As the inexperienced climbers used these strategies less, there was less energetic holdover for the next climbing cycle (Larson & Stern Jr, 1986). All participants maintained overhead postures around 120° of elevation during most of the climb cycle. Climbing is highly reliant on the exceedingly flexible human shoulder, particularly elevation (Lewis et al., 2001). This is notable, as overhead postures place a high risk of joint disorders on the shoulder complex (Ebaugh et al., 2006, Maciukiewicz et al., 2016; Rashedi et al., 2014). Upwardly directed reaches are also very demanding on the shoulder (Jonsson, 1988; Maciukiewicz et al., 2016), and may result in higher muscular demands. Considering the high muscular activation required to complete the task, it was clearly a difficult undertaking even for experienced climbers, owing to the gravitational loads and overhead reaching postures required. It is highly likely that prolonged horizontal bimanual arm-suspension climbing as performed in this scenario would lead to rapid fatigue and dyskinesis (Dickerson et al., 2015; Ebaugh et al., 2006). Despite humans demonstrating similar kinematic and muscular strategies and capabilities as chimpanzees, the workload of climbing is high in modern humans.

The postures assumed while climbing are concerning as they are likely to increase risk for upper extremity injuries. Humans are at a high risk for soft tissue injury and joint disorders in overhead postures (Chopp et al., 2010; Cote & Bement, 2010; Marras et al., 2006). One mechanism of injury initiation is fatigue of the rotator cuff muscles. Once fatigued, these muscles are unable to counter the superior pull of the deltoids and superior migration of the humeral head and decrease of the subacromial space occurs (Chopp et al., 2010; Lewis et al., 2001). This can cause mechanical impingement of tissues in the subacromial space. Chimpanzees and other climbing primates have a much larger rotator cuff and wider subacromial space than humans relative to the rest of their shoulder musculature (Potau et al., 2009; Roberts, 1974; Santago et al., 2015). In particular, the rotator cuff is of similar volume as the deltoids in chimpanzees, whereas the deltoids are relatively larger in humans (Carlson, 2006; Potau et al., 2009). In chimpanzees, this may mitigate the early onset of fatigue in the rotator cuff muscles before deltoid fatigue that is observed in humans, and prevent high risk for subacromial impingement in overhead postures. The relatively small size of the human rotator cuff and narrower subacromial space point to the habitual low workloads humans have evolved to perform using their upper extremity (Walker, 2009).

The bimanual climbing task represents a more extreme overhead task and exposure than typical, lower force modern overhead postures. However, evolutionary modification of the upper extremity has increased the musculoskeletal injury risk of all modern overhead behaviors. Modern human overhead behaviors are often a low force push or pull task. Performing these tasks above 90° of shoulder flexion or abduction is strongly associated with the development of shoulder disorders (Punnett et al., 2000). As arm elevation increases, activity of the shoulder muscular increases and muscular fatigue becomes likely to occur (Anton et al., 2001; Sood et al., 2007). When overhead postures are repetitive and include axial rotation of the arm, the risk of fatigue and shoulder injury amplifies (Hughes et al., 1997; LeClerc et al., 2004). Muscular fatigue of the shoulder musculature, particularly the rotator cuff, routinely occurs in occupational settings requiring repetitive, overhead postures with low hand loads (Ebaugh et al., 2006; Nussbaum et al., 2001; Sood et al., 2007). The present overhead task represents a more extreme range of human shoulder function by combining overhead postures with high hand force. Overhead postures of both high and low hand loads require high amplitude contribution from the shoulder musculature, which can lead to fatigue and injury. The overhead example provided in the present study contributes to, and is in agreement with the biomechanical and ergonomic research on overhead behaviors in humans.

While climbing may have been an ancestral mode of locomotion, it is a difficult and highly variable behavior in modern humans. Climbing experience increased the likelihood of kinematics and muscular strategies that more closely mimic climbing primates. However, experience did not reduce muscle activity to more sustainable levels, or lead to predictable population-level muscle activation patterns, as seen in human walking, our primary present form of habitual locomotion (Wood & Richmond, 2000).). The high variability may indicate that muscle redundancy at the shoulder enables various climbing muscle patterns. As none of the current study participants partook in climbing activities beyond a few hours a week, it remains to be seen whether habitual climbing in modern humans would lead to less variable climbing behaviors that are similar to recorded primate behaviors. The average activation level required to complete the present task was very high in both participant groups, which would make attempts to become habitual climbers difficult without incurring fatigue-related injuries. Up to 90% of competitive and recreational climbers suffer an upper extremity overuse injury, with anywhere from 33-50% of these injuries occurring at the shoulder (Rooks, 1997; Wright et al., 2001). This is an indication that these behaviors are quite difficult to perform habitually with the modern human upper extremity.

3.8.4 Limitations

There are a number of limitations to the present study. Both participant groups were very fit. Therefore, the climbing strategies recorded do not represent most of the entire human population. Actual novices were not included as they would likely not complete the task, feel comfortable with the task, or would have been at a high risk for injury during the laboratory visit. Had they been included, the between group results may have been more stark. Of the experienced group, none of the climbers were experienced specifically in horizontal bimanual arm-suspension climbing, but rather in a variety of rock climbing, wall climbing, and bouldering.

Therefore, both participant groups could be considered inexperienced in the specific task tested, with one group having more experience in generalized overhead, weight-bearing tasks. Inclusion of other populations exhibiting proficiency in overhead weight-bearing and bimanual arm-suspension, such as gymnasts, could benefit future research. The rung spacing was fixed in the present study. While this choice mimicked primate studies, the anthropometric variability of the human participants in the present study could have affected the ability of each to perform the task. Some of the kinematic and EMG variability could be explained by the fixed rung spacing. A further study with modifiable rung spacing, or correlation of subject specific anthropometrics, such as arm length, with kinematic and muscular strategies could provide greater insight into bimanual climbing task variability by removing a confounding factor in the present study. Further, research into other forms of brachiation would also be beneficial. The present bimanual climbing task was used to mirror chimpanzee studies to allow between species comparisons. However, understanding the three-dimensional biomechanics of other, more common arboreal methods, like rock climbing and quadrupedal climbing, would be both clinically and evolutionarily relevant. The present kinematic analysis did not include scapular and clavicular kinematics. These bones were tracked during the data collection phase, but due to technical limitations, it was impossible to reliably reconstruct these bones and derive relative three-dimensional rotations. Climbers have altered static scapular rotations compared to non-climbers (Roseborrough & Lebec, 2007). Analyzing dynamic three-dimensional scapular kinematics would be a highly useful clinical, biomechanical, and physical anthropological endeavor. Similarly, not all muscles surrounding the shoulder were collected. Muscles not considered due to methodological capacity and constraints include some considered important to climbing, such as parts of the deltoid, trapezius and rotator cuff.

The qualitative between species comparisons relied on a number of assumptions, which limit their interpretation and generalizability. Different statistical assessments were performed for the within-human and between-species analyses of kinematics. Owing to the unavailability of variability for chimpanzee kinematics, the between-species kinematic analysis chosen determined whether the single chimpanzee sample was within the standard deviation bands of the human sample. This assessment did not consider whether a mean curve was different between species, but rather whether the chimpanzee kinematics could fall within the collected human population. Therefore, it is still possible that the two species could have different two-dimensional mean angle waveforms that remained undetected in the present analysis. Additionally, while the two-dimensional kinematics give insight into whether three-dimensional kinematics would be similar between species, they cannot be used to conclusively indicate three-dimensional kinematic statistical non-significance between humans and chimpanzees (Winter, 2009). The results qualitatively indicate the similarity between species. As limited chimpanzee data exists, using a two-dimensional kinematic analysis remains the best indicator of similarities between chimpanzees and human horizontal bimanual arm-suspension climbing kinematics. The between-species kinematic similarity provides the justification to substitute modified human three-dimensional motion data as the postural inputs for a chimpanzee computational model. Finally, the muscular comparison was qualitative and only considered the general phasic timing of bursts of activity. The amplitude and specific timing of muscle activity could not be considered due to differences in the collection and processing of the species-specific EMG data. The qualitative analysis gives insight into the overall similarities between species in muscle recruitment patterns, but does not provide an opportunity to examine the specific, nuanced, evolved differences between species.

3.9 Conclusion

Bimanual climbing is a difficult task for modern humans. Of the two participant groups studied, those experienced with climbing overall used slightly more efficient climbing kinematics and reduced muscular activity. Some of these strategies were similar to those reported and observed in primates that climb as a form of locomotion. Strong similarities were found between humans and chimpanzees performing the same climbing task, including the pendular-type swing used in more difficult climbing tasks, though humans maintained high muscle activity overall and the deltoids have different actions in the two species. Evolutionary changes to musculoskeletal morphology has made climbing a difficult, and even an injury-riddled behavior in modern humans (Lewis et al., 2001; Potau et al., 2009; Rooks, 1997). The muscular workload required to climb is extremely high, and likely unsustainable for long periods of time without the onset of fatigue and fatigue-related musculoskeletal disorders (Lewis et al., 2001). However, the shared ancestry of humans with brachiating primates makes bimanual climbing a feasible task to complete in modern humans. That humans have devolved the anatomy to locomote as climbers demonstrates our adaptations to low load, repetitive upper extremity tasks (O’Neill et al., 2017). Further research on comparative evolutionary locomotion and climbing, including computational musculoskeletal modeling, could explain why specific musculoskeletal adaptations evolved at the human shoulder in the face of concurrently increased rotator cuff pathology.

Chapter 4 Study 2: Estimation of Shoulder-specific Geometric Constraints in Chimpanzees: Scapular Rhythm and Glenohumeral Dislocation Ratios

4.1 Introduction

Computational musculoskeletal models typically include multiple parts or modules to represent complex biomechanical behaviors. One of these parts is the geometric rendering of the system. A geometric module typically involves the description of bone shapes and orientation with respect to each other, as well as placement of the muscles on these bones via the definition of orthopedic origin and insertion sites. Musculoskeletal geometry is also depicted in muscle force prediction modules. These modules often employ optimization routines and mathematical descriptions of musculoskeletal geometric constraints to predict muscle forces. This includes definition of physiological and architectural features of the musculature that acts at the region. Combining this data enables the geometric construction of the musculoskeletal model.

Depending on the joints or body regions being modeled, other geometric parameters and constraints may also require mathematical representation. Specific to the shoulder is modeling the biomechanics of shoulder rhythm and the intrinsic stability of the glenohumeral joint (Dickerson, 2007; Makhsous, 1999; Veeger & van der Helm, 2007). In primates, the shoulder is a multi-joint region that comprises a closed-linked chain of movements between several moving boney parts. The predictable relationship between these moving parts is termed the shoulder rhythm. Joint stability is inherent within the boney structure and orientation of a joint. However, as is the case with the relatively unstable glenohumeral joint, static joint stability can be supplemented by additional mechanisms to prevent dislocation and pathological movement.

Shoulder rhythm is defined as the three-dimensional rotations of the scapula and clavicle concomitant with a given thoracohumeral movement (Inman et al., 1944).

Shoulder rhythm is a phenomenon that occurs due to the scapula and clavicle being detached from the ribcage and able to move freely about the thorax. Measurement and understanding of shoulder rhythm has many hurdles. These include the difficulty of dynamically tracking the movement of the scapula *in vivo*, as well as the multitude of scapular orientations that can exist for a given thoracohumeral posture (Matsen et a., 1994). Study of shoulder rhythm has helped elucidate how the linked rotations of the scapula and clavicle are associated with humeral and thoracic orientations, and aid in the large range of motion of the shoulder in humans. Using the predictable three-dimensional rotations of the scapula and clavicle with a specified arm movement, shoulder rhythm has been mathematically represented in humans through regression (Grewal & Dickerson, 2013; Makhsous, 1999). Computational modeling of shoulder rhythm provides the means to realistically model the rhythm that provides motion at the shoulder that is necessary for model realism without direct measures of scapular and clavicular orientations.

Stability of the glenohumeral joint is multifaceted. The orientation and shape of the glenohumeral joint alone does not provide the stability necessary for effective joint movement. Many other features specific to the shoulder combine to provide stability throughout movement. These include muscle activations, articular version, ligament tension, the labrum, joint suction and adhesion/cohesion mechanics, proprioception and a negative internal joint pressure (Cole et al., 2007; Veeger & van der Helm, 2007). Together, these mechanisms provide stability to the flexible and mobile glenohumeral joint. The specific contribution of each mechanism and their combined influence to joint stability is unknown.

As each contributing component of shoulder stability is incompletely understood, incorporating the various parts of shoulder stability into a musculoskeletal model requires a different approach than considering each separately. A mathematical, composite rendering of shoulder stability is created by computing an overall joint stability quotient, based on dislocation-level and direction-specific shear and compressive force ratios (Lippitt et al., 1993). Stability is defined as the proportion of shear force permissible in a given direction while a compressive force is directed into the joint fossa. Compression is mostly produced through muscular action, though some of the other stabilizing methods can also contribute (Dickerson, 2008; Veeger & van der Helm, 2007). This produces direction-specific ratios of stability and dislocation likelihood in the glenohumeral joint. Such ratios have been calculated in the human glenohumeral joint using cadaveric material (Lippett et al., 1993). Dislocation ratios provide a pragmatic means to modeling stability at the glenohumeral joint in the context of limited data on the individual contributory mechanisms.

Both shoulder rhythm and stability ratios have been quantified in humans, but not chimpanzees. Shoulder rhythm has typically been measured using motion capture or medical imaging, while glenohumeral stability ratios have typically been determined on tissue tolerance analyses of cadavers. No such analyses have been conducted on chimpanzees. Access to chimpanzees, both *in vivo* and *in vitro*, is limited. While research on these primates was once common due to their close genetic relationship to humans, modern ethical discourse makes scientific research on live chimpanzees highly restrictive. Chimpanzees are also an endangered species. Species conservation has taken precedence, ensuring preservation and prosperity of remaining populations of chimpanzees, both in the wild and captivity. While the most valid means of determining geometric shoulder parameters in chimpanzees, including shoulder rhythm and glenohumeral stability, would be through measurement on live specimens, this is not currently feasible. However, available information regarding these geometric parameters in humans and morphological differences and similarities between chimpanzees and humans provide a means of estimating chimpanzee shoulder rhythm and glenohumeral stability.

4.2 Purpose

The purpose of this study was to estimate the chimpanzee shoulder rhythm and stability ratios of the glenohumeral joint by modifying presently used human mathematical representations of these biological phenomena. Modifications were made through mathematical quantification of relevant morphological differences between chimpanzees and humans in upper extremity bone shape and orientation, kinematics, and glenoid shape and depth. Scanned chimpanzee shoulder bones were used to create a digital model to estimate chimpanzee shoulder rhythm in a series of static postures. Along with literature sources, scanned scapulae of both a human and chimpanzee were used to estimate changes to glenohumeral shape depth to estimate chimpanzee glenohumeral stability ratios. The study flow is outlined in Figure 33.

4.3 Objectives

Objective one – Through regression analysis, develop a chimpanzee shoulder rhythm, guided by existing data, including the DIESEL human shoulder rhythm, chimpanzee shoulder x-rays, and published morphological data.

Objective two – Determine appropriate stability ratio offsets for the chimpanzee glenohumeral joint based on morphological differences between the two species in glenoid shape and depth.

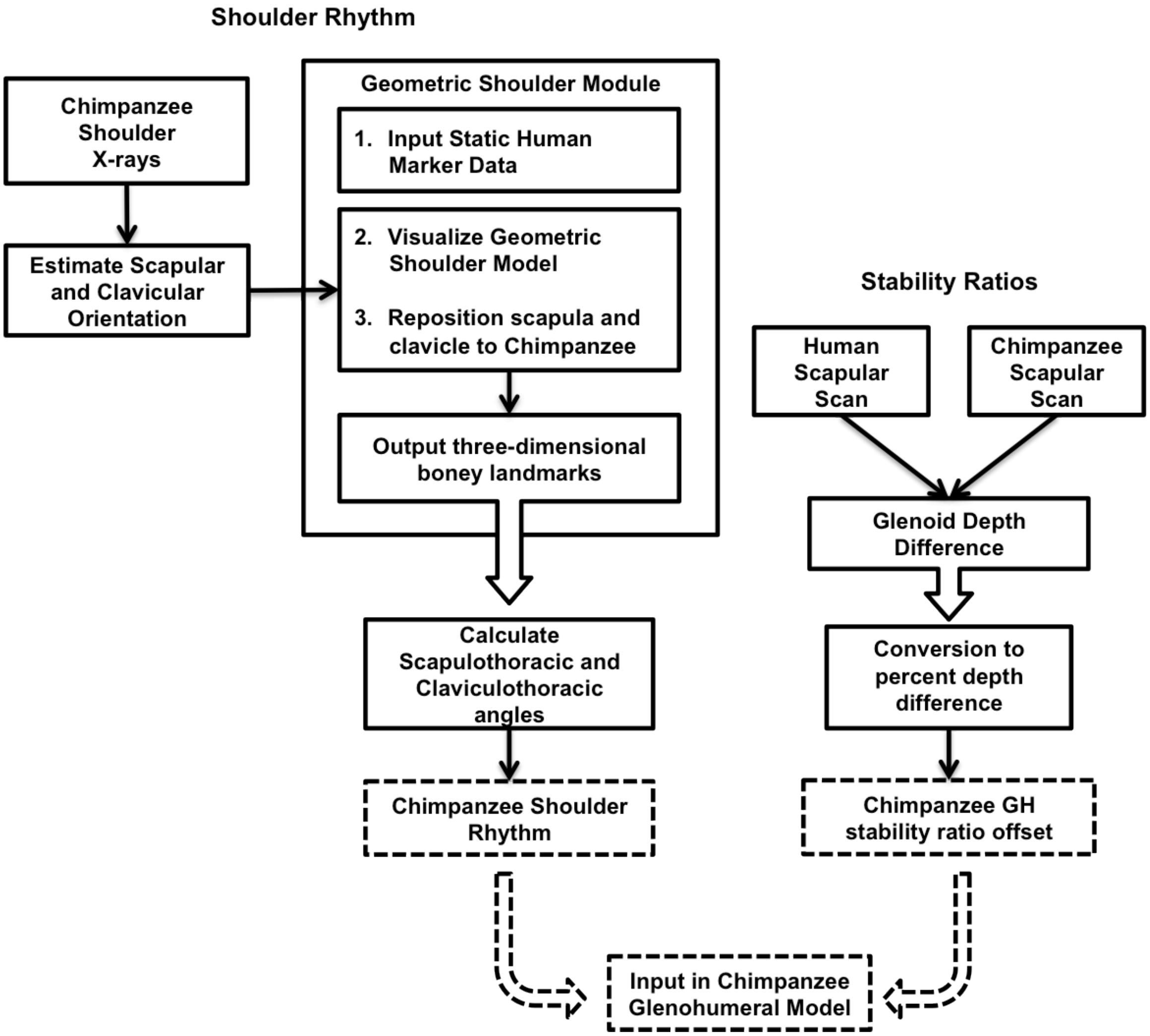


Figure 33: Flowchart separately outlining the Study 2 procedures for determining the chimpanzee shoulder rhythm and glenohumeral (GH) stability ratios. Dashed lines represent final geometric values used in the development of the chimpanzee glenohumeral model.

4.4 Shoulder Rhythm Methods

Development of the chimpanzee shoulder rhythm required a hybrid approach using human data, and limited available data on chimpanzee scapular and clavicular orientations. The Geometric Module of the Chimpanzee Glenohumeral Model was constructed and used as the apparatus for estimating three-dimensional chimpanzee scapular and clavicular orientations from a series of static thoracohumeral postures. Initially static human thoracohumeral postural data were applied as module inputs, and the human shoulder rhythm was used to derive chimpanzee scapular and clavicular orientations. The initial orientations were visualized through the geometric module. Using the geometric module visual of the shoulder complex, the chimpanzee scapular and clavicular orientations were iteratively rotated until the bone orientations were reflective of chimpanzee shoulder x-ray images. Once the chimpanzee scapular and claviclar orientation satisfied the chimpanzee x-rays, landmark three-dimensional positions were recorded from clavicle, scapula, humerus and thorax. The landmarks were used to derive chimpanzee thoracohumeral, scapulothoracic and claviculothoracic joint angles. Finally, the angles were used to calculate six regression equations representing three scapular and three clavicular rotations that compose the chimpanzee shoulder rhythm.

4.4.1 Methods: Development of Chimpanzee Shoulder Rhythm

4.4.1.1 Implementation of Human Shoulder Rhythm Data into Chimpanzee Geometric Module

A set of equations for a novel human shoulder rhythm was generated by the DIESEL research group at the University of Waterloo (Grewal & Dickerson, 2013). These equations were derived from experimentally measured scapular and clavicular positions during static arm elevations (Grewal & Dickerson, 2013). Scapular and clavicular orientations can be estimated using these equations with a known thoracohumeral orientation. The benefit of the novel shoulder rhythm is it was developed to include axial humeral rotation and a greater range of humeral postures, including overhead postures (Grewal & Dickerson, 2013). This is important for the present purposes of modeling and analyzing brachiation in humans and chimpanzees. Brachiation postures require overhead postures and axial rotation of the arm (Larson, 1988; Larson & Stern, 2013; Usherwood et al., 2003).

Initially the new DIESEL shoulder rhythm was incorporated into the chimpanzee geometric module using the current equations for scapular and clavicular three-dimensional rotations (Equations 1–6). The coefficients of the linear and, in the case of clavicular elevation/depression, quadratic regression equations are multiplied by the relative thoracohumeral orientations calculated using the Euler angle method (Grewal & Dickerson, 2013). These equations provided initial estimates for chimpanzee scapular and clavicular orientations. From the initial estimates, modifications were made to scapular and clavicular orientations to develop a set of novel chimpanzee shoulder rhythm equations.

Alterations to the position of the scapula and clavicle between humans and chimpanzees are imperative, due to both the morphological divergences in each bone, as well as the torso. Features such as clavicle length, scapular length and thoracic shape, while loosely associated with locomotor behaviors, are strongly associated with ranges of shoulder motion (Schmidt & Krause, 2011). The shape of the chimpanzee torso is cone-shaped, with a diameter that decreases inferiorly to superiorly. This changes the position of the scapula to more anterior tilt and lateral rotation (Lewis et al., 2001). The clavicle is also distally elevated and superiorly rotated in chimpanzees (Bramble & Lieberman, 2004). These anatomical differences influenced the three-dimensional reorientation and trajectory of the chimpanzee scapula and clavicle from the initial human shoulder rhythm predictions.

Equation 1: Equation predicting the scapular rotation of retraction/protraction (γ). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are plane of elevation ($\gamma_{TH0)}$, elevation (β_{TH}), and internal/external rotation (γ_{TH1}) (Grewal, 2012).

$$\gamma_S = 30.1 + (0.18\ \gamma_{TH0}) + (-0.032\ \beta_{TH})\ (\gamma_{TH0} - 26.9)(\beta_{TH} + 77.7)(-0.001)$$

Equation 2: Equation predicting the scapular rotation of lateral/medial rotation (β). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are plane of elevation ($\gamma_{TH0)}$, elevation (β_{TH}), and internal/external rotation (γ_{TH1}) (Grewal, 2012).

$$\beta_S = -1.68 + (0.034\ \gamma_{TH0}) + (0.238\ \beta_{TH}) + (-0.017\ \gamma_{TH1}) + (\gamma_{TH0} - 26.9)(\gamma_{TH1} + 24.4)(-0.001)$$

Equation 3: Equation predicting the scapular rotation of anterior/posterior tilt (α). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are plane of elevation ($\gamma_{TH0)}$, elevation (β_{TH}), and internal/external rotation (γ_{TH1}) (Grewal, 2012).

$$\alpha_S = -11.2 + (0.05\ \gamma_{TH0}) + (-0.298\ \beta_{TH}) + (-0.021\ \gamma_{TH1})$$

Equation 4: Equations predicting clavicular rotation of elevation/depression (γ), The three thoracohumeral rotations used to predict the scapular and clavicular rotations are plane of elevation ($\gamma_{TH0)}$, elevation (β_{TH}), and internal/external rotation (γ_{TH1}) (Grewal, 2012).

$$\gamma_C = -13.3 + (0.073\ \gamma_{TH0}) + (0.358\ \beta_{TH}) + (0.035\ \gamma_{TH1})$$

Equation 5: Equations predicting clavicular rotation of retraction/protraction (β). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are plane of elevation ($\gamma_{TH0)}$, elevation (β_{TH}), and internal/external rotation (γ_{TH1}) (Grewal, 2012).

$$\beta_C = -14.6 + (0.057\ \beta_{TH}) + (0.002\ \beta_{TH}^2) + (-0.031\ \gamma_{TH1})$$

Equation 6: Equations predicting clavicular rotation of forward/backward rotation (α). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are plane of elevation ($\gamma_{TH0)}$, elevation (β_{TH}), and internal/external rotation (γ_{TH1}) (Grewal, 2012).

$$\alpha_C = 0.411 + (-0.016\ \gamma_{TH0}) + (-0.201\ \beta_{TH}) + (0.03\ \gamma_{TH1}) + (\beta_{TH} + 77.7)(\gamma_{TH1} + 24.4)(-0.0007)$$

Human thoracohumeral angles were used as initial kinematic inputs in the chimpanzee geometric module to predict scapular and clavicular orientations. The shoulder rhythm from the DIESEL regression equations required relative thoracohumeral angles. However, there was no previously collected three-dimensional upper extremity data that would suffice as inputs to enable the shoulder rhythm calculations. Nor are there laboratories that are equipped and authorized to conduct three-dimensional biomechanical analyses of the chimpanzee upper extremity. For this reason, human thoracohumeral rotations were used as inputs to the chimpanzee geometric model and aided in deriving the initial chimpanzee scapular and clavicular orientations. The thoracohumeral inputs serve as an initial input to the geometric module only. Subsequent alterations to the chimpanzee shoulder rhythm systematically improved the representation of the orientations of the chimpanzee scapula and clavicle. As such, the decision to use human data as the initial input was considered reasonable.

4.4.1.2 Collection of Chimpanzee Scapular and Clavicular Orientation Data

Along with human shoulder rhythm equations, chimpanzee x-rays were used as the foundation for estimating chimpanzee scapular and clavicular motion. Due to the lack of three-dimensional biomechanical data on chimpanzees, and particularly limited data on scapular and clavicular biomechanics, there are no current options for obtaining previously collected or novel chimpanzee scapular and clavicular orientation data. X-rays of chimpanzee shoulders were provided through Stony Brook University Department of Anatomy (Figure 34). These images were obtained from anesthetized chimpanzees lying prone on a table, and represent boney orientations with limited muscular contribution. X-rays provided a comparison to the image produced by the geometric module to determine if the scapular and clavicular placements were reasonable. Further assumptions were made on the position of the scapula and clavicle based on known human values, and differences in thoracic, scapular and clavicular morphology between the two species (Larson et al., 2000; Schmidt, 2005; Schmidt & Krause, 2011).

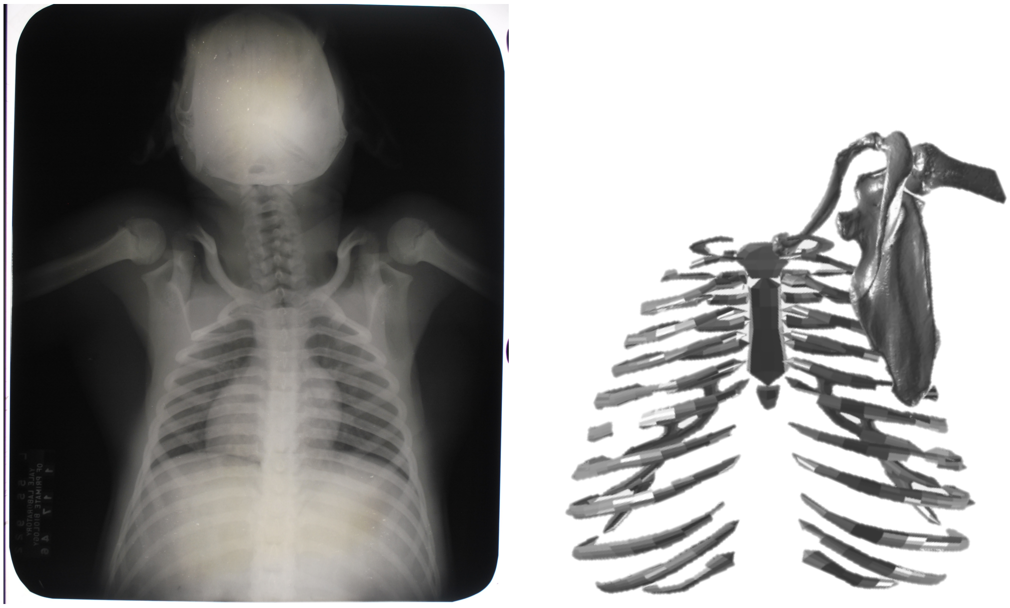


Figure 34: X-ray of upper extremity of an anesthetized chimpanzee (left), showing the faint outline of the scapula and clavicle. These x-rays were used to guide the placement of the scapula and clavicle in the digital model (right)

4.4.1.3 Evaluation and Correction of Chimpanzee Shoulder Geometry in Geometric Module

A series of 20 static arm configurations were represented with the chimpanzee geometric module. While these ranged in degree of elevation, plane of elevation and axial rotation, they primarily included a series of scapular plane increases in humeral elevation, and some overhead changes in humeral plane of elevation. These postures were extrapolated from two different data sets of reaching and bimanual climbing using Vicon (Oxford, UK) motion capture, collected in the DIESEL laboratory. Each individual static arm posture produced a static shoulder rhythm using the DIESEL human shoulder rhythm equations. A visual rendering of the chimpanzee geometric module for each of these static inputs allowed for evaluation of the accuracy and heuristic modification of the shoulder rhythm estimations with chimpanzee bones.

Due to the morphological differences between the species, the initial chimpanzee glenohumeral joint center of rotation position rendered in each static posture was not considered geometrically realistic, and was altered. A comparison of the positioning of the chimpanzee glenohumeral joint in the x-rays with those rendered by the DIESEL shoulder rhythm predictions indicated that the humeral head was too inferior and lateral in all postures. To correct this offset, the glenohumeral joint center and acromion data points in the kinematic input files were translated superiorly and medially to match the glenohumeral position observed in the chimpanzee x-rays in the static postures. This process was done iteratively in each static posture until the obtained glenohumeral position adequately represented the chimpanzee glenohumeral position.

To reorient the scapula and clavicle to represent an anatomically correct chimpanzee shoulder, the intercept values in equations 1-6 were altered. The intercept value represents the baseline resting orientation of the scapula and clavicle in three dimensions. As each equation determines a rotation about one of the three axes, axis-specific changes in degree of rotation were possible. Incremental changes were made until the orientation of both bones visually approximated realistic anatomical positions. This included an anterior/posterior tilt orientation that had the scapula resting against the thorax. This process was repeated for every static posture assessed through the geometric module.

4.4.1.4 Determination of Chimpanzee Landmarks and Joint Angles

Anatomical landmarking and chimpanzee joint angles were calculated following the correction of chimpanzee scapular and clavicular orientations in the geometric module. When the geometric module output approximated an anatomically correct chimpanzee shoulder, three to four anatomical landmarks were identified and digitized on each of the segments of the torso, scapula, clavicle and humerus (Figure 35). The three-dimensional values of each of these landmarks were recorded, and used to calculate relative joint angles using the Euler method for each of the 20 static postures. Local coordinate systems were created using international Society of Biomechanics (ISB) standards for the thorax, humerus, and clavicle (Wu et al., 2005). A modified version of ISB standards was used for the scapula. ISB dictates that the scapula z-axis is directed anatomically along the scapular spine. However, large differences exist between humans and chimpanzees in the orientation of the scapular spine. Chimpanzees have a superiorly oriented scapular spine (Figure 34), whereas humans have a laterally oriented scapular spine (Lewis et al., 2001). An ISB standard z-axis would redirect the z-axis in a superior-inferior direction, and have consequences on the direction of both other axes. Determining joint angles from this local coordinate system would create relative joint angles that were less clinically and biomechanically relevant or comparable to human joint angles (Grood & Suntay, 1983). As a result, the z-axis for the chimpanzee scapula local coordinate system was the cross product of an anatomical y-axis and x-axis.

From the local coordinate systems, thoracohumeral, scapulothoracic and claviculothoracic angles were calculated for all static postures using the Euler method.

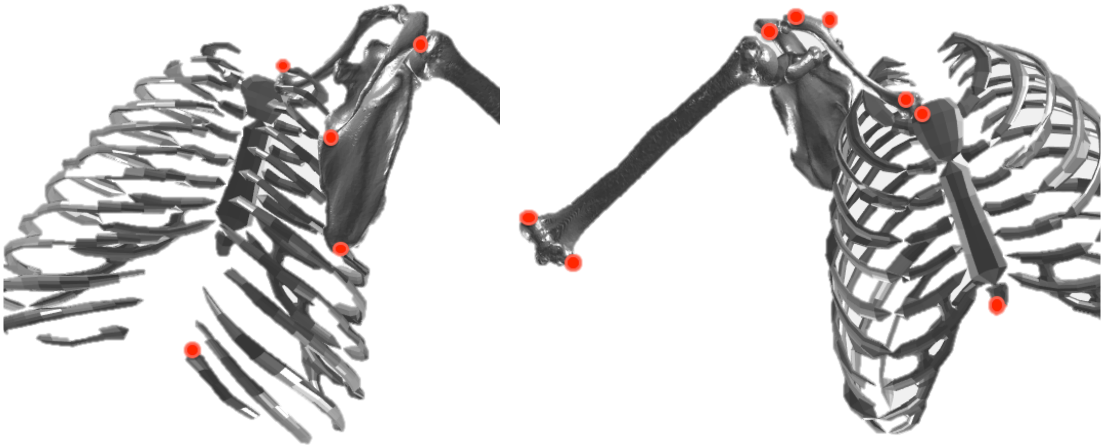


Figure 35: The anatomical landmarks selected on each of the four boney segments to create local coordinate systems. Three landmarks were digitized on the scapula, and clavicle, while a fourth anatomical landmark (anterior acromion) was digitized on the scapula to be the third humeral landmark. Four landmarks were digitized on the torso segment.

4.4.1.5 Development of a chimpanzee shoulder rhythm

The chimpanzee shoulder rhythm was derived two times, but only one derivation is presented. An initial attempt to produce a chimpanzee rhythm was done using an all-subsets regression model. This method selected the combination of variables that created the best fit model for each of the three scapula and clavicle equations. Any variable that contributed less than 2% to the explanation of the model was removed (Grewal, 2012). Due to the limited chimpanzee data set, this method produced higher order functions with anatomically unrealistic intercept values. The set of six equations produced by this analysis are in Appendix A. As these equations were considered anatomically unrealistic, they were not considered to be a representative estimation of the chimpanzee shoulder rhythm. Following this, a second approach was taken to derive the chimpanzee shoulder rhythm equations.

The chimpanzee shoulder rhythm equations were developed again through a regression analysis, using only the equation terms determined to be significant in the human regression equations (Grewal, 2012). A two-step regression analysis was used to predict scapulothoracic and claviculothoracic rotations from the three-dimensional thoracohumeral angles using only the coefficients from the previously derived human equations (Grewal et al., 2013). Resultantly, each of the six human and six chimpanzee shoulder rhythm equations had the same variables. This allowed a term-by-term comparison of the two species shoulder rhythm. The following set of *Chimp* shoulder rhythm equations were derived:

Equation 7: Equation predicting the chimpanzee scapular rotation retraction/protraction (γ). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\gamma_{S\_Chimp} = -3.91 + (0.354\ \gamma_{TH0}) + (-0.232\ \beta_{TH}) + (-0.0029\ \gamma_{TH0}\ \beta_{TH})$$

Equation 8: Equation predicting the chimpanzee scapular rotation lateral/medial rotation (β). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\beta_{S\_Chimp} = 20.28 + (0.0806\ \gamma_{TH0}) + (0.2087\ \beta_{TH}) + (0.0042\ \gamma_{TH1}) + (0.00103\ \gamma_{TH0}\ \gamma_{TH1})$$

Equation 9: Equation predicting the chimpanzee scapular rotation anterior/posterior tilt (α). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\alpha_{S\_Chimp} = 28.18 + (-0.0062\ \gamma_{TH0}) + (0.1017\ \beta_{TH}) + (0.029\ \gamma_{TH1})$$

Equation 10: Equation predicting chimpanzee clavicular rotation elevation/depression (γ). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\gamma_{C\_Chimp} = -4.2 + (0.283\ \gamma_{TH0}) + (0.145\ \beta_{TH}) + (0.1992\ \gamma_{TH1})$$

Equation 11: Equation predicting chimpanzee clavicular rotation retraction/protraction (**β**). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\beta_{C\_Chimp} = -40.52 + (0.249\ \beta_{TH}) + (0.0011\ \beta_{TH}^2) + (-0.1108\ \gamma_{TH1})$$

Equation 12: Equation predicting chimpanzee clavicular rotation forward/backward rotation (α). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\alpha_{C\_Chimp} = 67.0 + (0.136\ \gamma_{TH0}) + (0.245\ \beta_{TH}) + (0.1049\ \gamma_{TH1}) + (0.00109\ \beta_{TH}\ \gamma_{TH1})$$

4.4.2 Data Analysis of Chimpanzee Shoulder Rhythm

A comparison between the human and chimpanzee shoulder rhythm equations was conducted to determine the robustness of the chimpanzee shoulder rhythm, and how different it was from the human shoulder rhythm. The human and chimpanzee shoulder rhythm equations were assessed through an analysis of the r-squared values and RMS error between both. Both of these values give a measure of the strength of the fit of the regression line to the measured data. The r-squared value represents the degree to which each equation accounts for the variability in the data, while the RMS error gives a mean value for the distance of the measured data points from the predicted regression line values.

Following the initial analysis of r-squared and RMS values, a statistical comparison of human and chimpanzee shoulder rhythm coefficients was performed. Comparison with the statistical values obtained through the human shoulder rhythm derivation was performed to assess between species differences (Grewal, 2012). The chimpanzee data was statistically compared to the data sample from which the original DIESEL shoulder rhythm equations were derived. Data from both species were combined for the analysis, but identified as two different samples, creating a new regression variable of group. The regression analysis was performed again, deriving the same equations for both groups found in the *Chimp* and *Human* equations, while simultaneously determining significant difference between the two groups for all coefficients in all six equation. This method determined whether the chimpanzee shoulder rhythm was statistically different from the human shoulder rhythm by comparison of each of the equation coefficient at α=0.05.

4.4.3 Results

The six chimpanzee scapular and clavicular rotations followed similar trends to human boney rotations. The six boney rotations for both species – three scapular and three clavicular – are plotted against thoracohumeral elevation in Figure 36. Elevation was chosen as it represents the thoracohumeral rotation that has been widely observed while analyzing shoulder rhythm (Inman et al., 1944; Karduna et al., 2001). Elevation is associated with specific scapular and clavicular rotations, and was the main axis of rotation about which the chimpanzee data points were altered to produce the novel shoulder rhythm (Inman et al., 1944; Karduna et al., 2001; Ludewig et al., 2004; Lukasiewics et al., 1999; McClure et al., 2001).

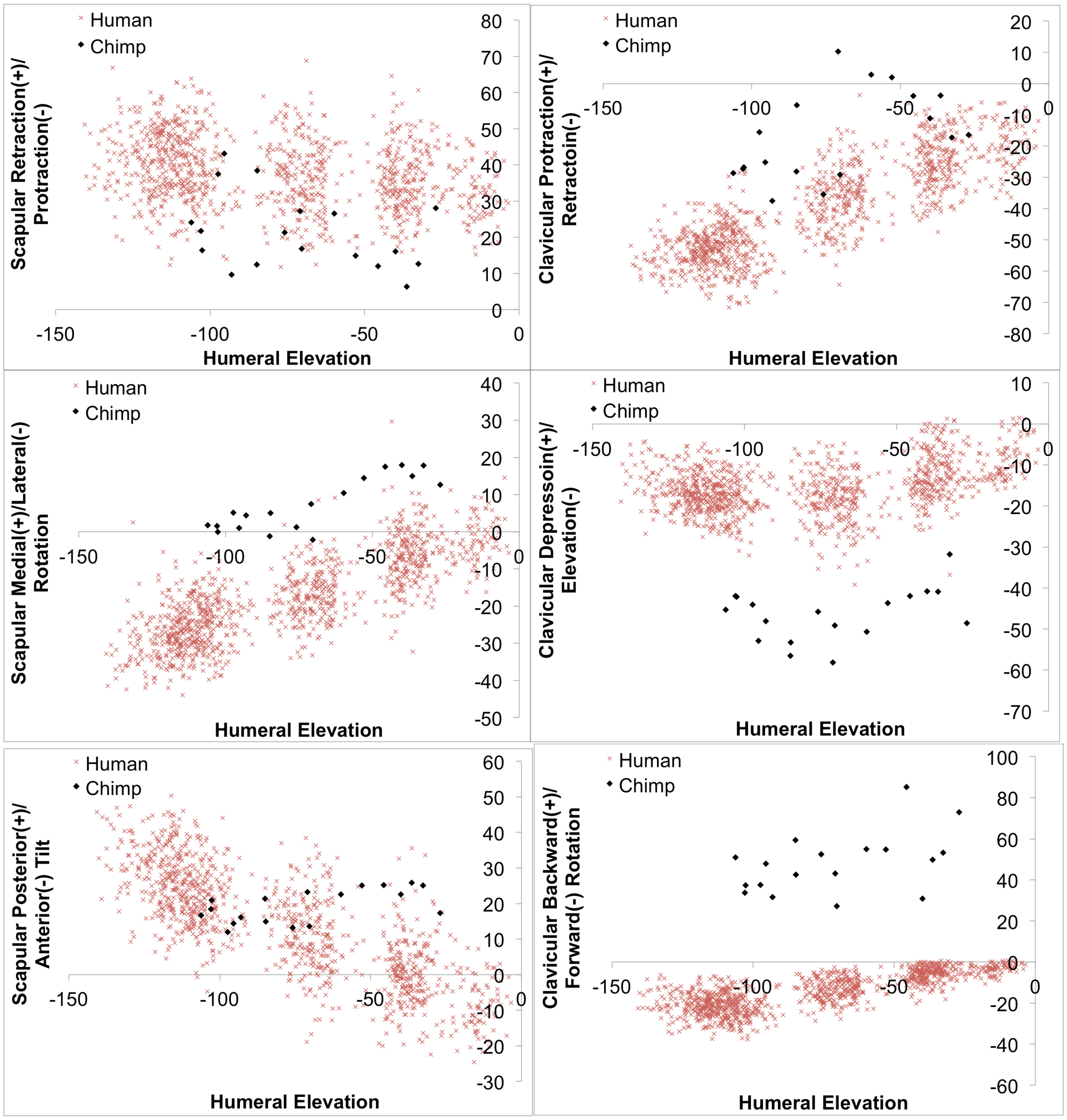


Figure 36: Scatterplots of the human (red) and chimpanzee (black) data sets for each of the three scapular and clavicular rotations.

There were notable similarities between the chimpanzee and human data sets. Scapular retraction/protraction and medial/lateral rotation had similar slopes in both species. Similarly, all three clavicular rotations had similar slopes in both species (Figure 36). In most of these examples though, especially in the clavicle, there was an offset between the species. The slope of the chimpanzee anterior/posterior tilt was very different from the human slope. In chimpanzees, there was very little change in anterior/posterior tilt with increasing elevation, contrasting with the increasing posterior tilt in humans (Figure 36).

4.4.3.1 Between-species Comparison of Shoulder Rhythm Intercept Values

The intercept values in Table 7 give an indication of how anatomically realistic and similar to humans the predictions were for the chimpanzee equations. These values indicate the scapular and clavicular orientation predicted by the equations with the arm in a resting position by the side, and are relative to the torso segment. In humans these values were no greater than 30° (Table 7). The *Chimp* equations predicted greater scapular medial rotation, β_S, and posterior tilt, α_S, than humans. The *Chimp* equations also had a greater resting elevation, β_c, and backward rotation, α_C, of the chimpanzee clavicle.

Table 7: A comparison of the intercept values for the chimpanzee equations and the human equations. These values give a sense of the anatomical realism of the baseline predictions of all the equations.

		γ_S	β_S	α_S	γ_C	β_C	α_C
Intercept	***Chimp***	-3.91	20.28	31.83	-4.2	-40.52	67.0
	Human	30.1	-1.68	-11.2	-13.3	-14.6	0.411

4.4.3.2 Between-species Comparison of Shoulder Rhythm Robustness

The fit of both equations was assessed from r-squared and RMS error values (Table 8).

Table 8: R-squared and RMS error values derived for each of the six chimpanzee and human shoulder rhythm equations. Both values give an indication of the fit of the equations between the two species.

		γ_S	β_S	α_S	γ_C	β_C	α_C
Chimp	R-squared	0.47	0.75	0.42	0.57	0.70	0.304
	RMS Error	8.37	4.03	3.96	10.29	3.94	14.1
Human	R-squared	0.6	0.8	0.82	0.89	0.74	0.84
	RMS Error	6.31	5.26	6.54	5.11	3.24	3.5

The chimpanzee regression analysis resulted in comparable or less strong fits than the human regression equations. The chimpanzee r-squared values were comparable or lower than the human analysis. Moderate to strong correlations existed for all six rotations, except clavicular forward/backward rotation, α_C, which had a weak correlation r-squared value of 0.3. In instances where the RMS value was equal or higher for the chimpanzee equations, there was more variability in the chimpanzee shoulder data than the human shoulder data with respect to the predicted equations. This was particularly true of the scapular and clavicular retraction/protraction, γ_S and γ_C,, both of which had much higher RMS error (Table 8). The chimpanzee scapular lateral/medial rotation, β_S, and anterior/posterior tilt, α_S, had a smaller RMS error, suggesting a tighter fit of the measured data with the regression line generated than for the human data set.

A final regression analysis examined group differences between *Chimp* and *Human* in each of the matching variable coefficients of the six regression equations derived. The p-values generated in this analysis, indicating statistical difference between species at $p<0.05$, are provided in Table 9.

Table 9: The differences between chimpanzees and humans for each of the variable coefficients and the intercept in the shoulder rhythms. A $p<0.05$ represents a significant difference between species.

Regression Term	γ_S	β_S	α_S	γ_C	β_C	α_C
Intercept	0.0001*	0.001*	0.0001*	0.222	0.003*	0.0001*
γ_{TH0}	0.130	0.749	0.791	0.104	0.714	0.154
β_{TH}	0.053	0.618	0.0001*	0.012*	0.716	0.681
β_{TH}^2	-	-	-	-	0.045*	-
γ_{TH1}	-	0.646	0.324	0.004*	-	0.0001*
$\gamma_{TH0}\,\beta_{TH}$	0.770	-	-	-	-	-
$\beta_{TH}\,\gamma_{TH1}$	-	-	-	-	-	0.891
$\gamma_{TH0}\,\gamma_{TH1}$	-	0.273	-	-	-	-

The intercept values, representing the baseline resting position of the scapula and clavicle, were very different between chimpanzees and humans in all equations except γ_C, clavicular retraction/protraction (Table 9). Beyond the intercept value, five of the equations had no more than one other variable significantly different between the two species. Retraction/protraction of the clavicle had two of three non-intercept terms different between species. Chimpanzees were predicted to retract and protract the scapula differently than humans for a given thoracohumeral posture. Aside from this one exception, the regression equations predicted very similar rotations in all three scapular and three clavicular rotations with given rotations in thoracohumeral rotations. This was a moderate indication that the equations predict chimpanzees will rotate their scapula and clavicle similarly to humans for similar thoracohumeral rotations.

4.4.4 Discussion

Objective one was achieved through the development of the *Chimp* shoulder rhythm equations. The greatest differences between the *Human* DIESEL and *Chimp* shoulder rhythm equations were found in the intercept values which represent resting positions. Some differences also exist in the equation variables coefficients, but these differences were less dramatic.

4.4.4.1 Evaluation of Species-specific Differences in Shoulder Rhythm

Determining the chimpanzee rhythm with the visual aid of two-dimensional. x-rays limited the visible dimensions of boney orientation. However, x-rays represented the best use of available data (Jenkins et al., 1978; Schmidt & Krause, 2011). The most visible rotations were lateral/medial rotation, β_S, of the scapula and elevation/depression, β_C, of the clavicle. As a result, these rotations were estimated first, with heuristic estimations of the other two rotations, followed by incremental changes of each rotation until an adequate orientation was obtained. Given this heuristic method, it is not surprising that the regression equations with the strongest fit are β_S and $\beta_{C.}$ All other rotations were based on less visual evidence from the x-rays and required more qualitative estimation. Given the similarities between human and chimpanzee shoulder morphology, the final chimpanzee shoulder rhythm equations represent a best estimate from limited data (Schmidt & Krause, 2011).

The chimpanzee regression equations were less robust that the human equations, which is likely attributable to influential factors. First, the chimpanzee data was limited to only a few discrete points on a single chimpanzee, while the human data had over 1000 data points from 28 participants. A small sample size increases the variability in an analysis (Miller, 2006). The limited chimpanzee data means a few outlier data points had a greater influence over the final estimate, increasing the RMS error and reducing the fit of the regression equation. Second, the chimpanzee data was also derived through qualitative estimation based on comparison with two-dimensional x-ray images. Determining tilt of the scapula and axial rotation of the clavicle was extremely limited from the x-rays and was estimated based on the estimated rotations of lateral/medial rotation, retraction/protraction and elevation/depression from the x-ray images and the shape of the ribcage. That these were the least reliable equations generated is likely due to measurement limitations. Though they were not as strong, the r-squared values reported in the *Chimp* equations are reasonable, and have been reported in human shoulder rhythm derivations previously (Xu Xu et al., 2014).

Resting scapular and clavicular orientations were the most significant difference between species in the shoulder rhythm equations, and relate to structural, morphological differences between species. The resting values for each of the chimpanzee shoulder rhythm equations were different than the humans by between approximately 10° and 65°. Differences in scapular resting positions were specific to the torso shape. Chimpanzees have a funnel shaped torso, whereas humans have a barrel shaped torso (Swindler & Wood, 1973). The chimpanzee torso narrows inferior to superior, and the scapula must reorient to accommodate this change in torso shape (Lewis et al., 2001; Roach & Richmond, 2015). Differences in torso shape account for some of the approximately 20° difference in the resting orientation of the scapula in all axes between species. The clavicle resting position was also significantly different between species, with the chimpanzee clavicle being more elevated and backwardly rotated. Chimpanzees have an elevated glenohumeral joint that gives the appearance of an elevated, shrugged shoulder

(Larson, 2007; Larson et al., 2007; Lewis et al., 2001). The clavicle elevates to physically meet the elevated acromion (Roach & Richmond, 2015; Voisin, 2006). Differences between species in axial rotation of the clavicle may be correlated with differences in elevation. As the human clavicle elevates, it forwardly rotates, until reaching overhead postures, where elevation slows and axial rotation continues (Grewal & Dickerson, 2013). The difference in resting axial rotation between the two species may have been due to the increased resting elevation of the clavicle in chimpanzees.

Some differences between humans and chimpanzees in resting boney orientation may be explained by measurement choices. Chimpanzees had a more retracted, medially rotated and posteriorly tilted scapula in resting position. The medial rotation and posterior tilt would seem surprising, particularly for a primate that has a more superiorly orientated glenoid (Lewis et al., 2001; Macias & Churchill, 2015), as lateral rotation would provide more superior orientation. As the angles described are the scapula and clavicle relative to the torso, the rationale for these baseline values lies in the local coordinate systems used to determine relative joint angles. A modified ISB coordinate system was used on the scapula, with a z-axis that was directed laterally across the body of the scapula instead of along the superiorly oriented scapular spine (Figure 37) (Wu et al., 2005). Relative to the position of the ISB compliant torso coordinate system, resting scapular coordinate system was closely in line with the torso. Therefore, medial rotation about the x-axis and posterior tilt about the z-axis would only marginally rotate the scapula inferiorly and posteriorly with respect to the torso, and would still leave the glenoid very superiorly oriented (Figure 37).

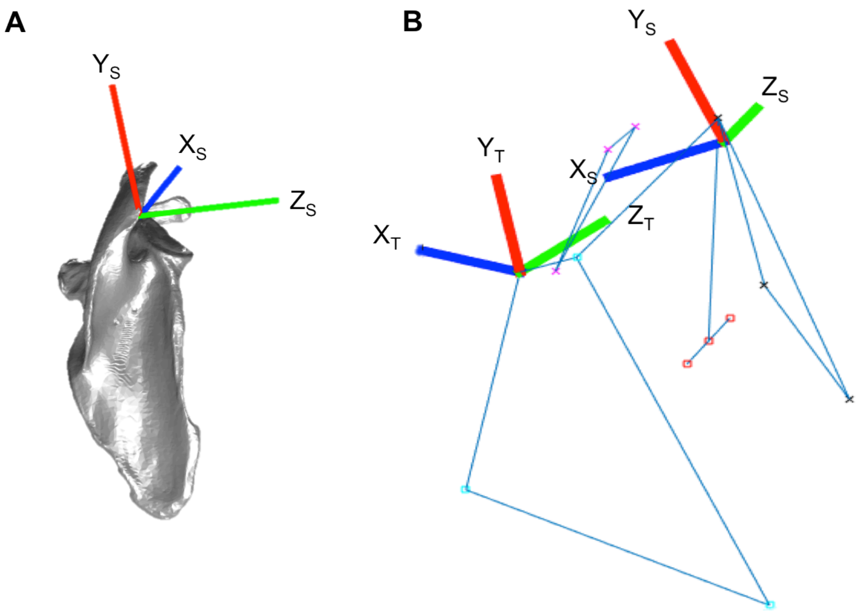


Figure 37: Chimpanzee scapula with a modified ISB coordinate system (A), and a resting arm position and the corresponding orientations of the torso and scapular local coordinate systems (B).

4.4.4.2 Influence of a Novel Chimpanzee Shoulder Rhythm

Shoulder rhythm has never been documented in chimpanzees, though it should exist based on orthopedic anatomy. Shoulder rhythm provides stability at the shoulder through coordinated movement of the clavicle, scapula and humerus (McClure et al., 2001). The results of this study suggest the presence of a common shoulder rhythm in chimpanzees. Humans and chimpanzees are closely related and have an upper extremity that is relatively similar (Lewis et al., 2001; Pronk, 1991; Wood & Richmond, 2000). Given the behaviors chimpanzees and humans engage in, both would exhibit similar ranges of motion to include both overhead, underhead and anterior-to-the-body postures. Many upper extremity behaviors overlap between species (Wood & Richmond, 2000). Once the resting position offset is removed, this overlap in behaviors translates into similar scapular and clavicular rotations to accommodate the similar ranges of motion. However, the primary behaviors conducted in these ranges of motion are often dissimilar between chimpanzee and humans, and may account for some of the differences between species.

There is limited data available on the shoulder rhythm and motion of primates. Gross differences in scapular and clavicular resting positions have been documented between primate families (Roach & Richmond, 2015; Schmidt, 2005; Schmidt & Krauss, 2011; Voisin, 2006). Hominoids, which include humans and chimpanzees, share a common scapular and clavicular organization, with similar clavicular shape, a scapula that remains posterior throughout range of motion, and a scapular orientation that allows horizontal abduction of the arm (Roach & Richmond, 2015; Schmidt & Krauss, 2011; Voisin, 2006). Humans and chimpanzees also share their shoulder structure with Ateles (Schmidt & Krauss, 2011). Two-dimensional scapular rotation and shoulder motion has been examined during quadrupedal walking and some brachiation in small primates of the Ateles family, such as lemurs, squirrel monkeys and spider monkeys (Jenkins et al., 1978; Schmidt, 2005; Schmidt & Fischer, 2000; Schmidt & Krause, 2011). Scapular motions in these primates are similar to chimpanzees and humans, as lateral/medial rotation is greater than other scapular rotations, and accounts for the greatest degree of change in arm elevation (Magermans et al., 2005; Schmidt, 2005; Schmidt & Krause, 2011). Though limited, the research on scapular motion in similar primates to chimpanzees and humans is in agreement with the results of the present study.

The greatest differences between species were in resting orientation of the scapula and clavicle, which are the result of primary behavioral differences and related structural differences. Shoulder rhythm is necessary for controlling arm range of motion, stabilization of the glenohumeral joint and maintenance of optimal muscle action (McClure et al., 2001). While the absolute range of motion available for the arm is similar in chimpanzees and humans, chimpanzees habitually use the shoulder in weight-bearing overhead brachiation and terrestrial quadrupedalism postures (Cartmill & Smith, 2009; Schmidt & Krause, 2011; Wood & Richmond, 2000). This has prioritized the chimpanzee shoulder for weight-bearing postures over a wide range of motion. Quadrupedal terrestrial locomotion is mostly limited to arm extension in a small range of motion, requiring a constrained amount of scapular and clavicular motion to be performed (Whitehead & Larson, 1994; Schmidt, 2005).

Brachiation, on the other hand, requires a greater range and variety of arm motions to perform (Jenkins et al., 1978). Resultantly, chimpanzees have a shoulder rhythm that increases structural stability through articular version and accommodates the large range of arm elevation and abduction necessary for brachiation (Lugo et al., 2008; Schmidt & Krause, 2011; Veeger & van der Helm, 2007; Wood & Richmond, 2000). These resting orientations allow chimpanzees to perform overhead postures using the glenohumeral joint with greater ease than humans (Lewis et al., 2001). Humans have a non-weight-bearing upper extremity with fewer habitual overhead behaviors (Ludewig et al., 2009). Though capable of more range of motion, humans are more likely to habitually use their shoulder in below-shoulder postures and the human shoulder rhythm prioritizes this motion. The human shoulder resultantly has a more medially rotated scapula and less elevated clavicle, both of which laterally orient the glenoid. While this provides less intrinsic stability from articular version, it prioritizes efficiency for the non-weight-bearing tasks of daily human living (Ludewig et al., 2009).

4.4.4.3 Limitations

There are a number of limitations to the methodology for deriving the chimpanzee shoulder rhythm. The chimpanzee shoulder rhythm was not directly measured, but was inferred based on a number of assumptions, which limit its generalizability. X-rays only provided two-dimensional evaluation of the chimpanzee scapular and clavicular position and orientation. Further, x-rays only provided a qualitative tool for estimating scapular and clavicular orientation. Chimpanzee scapular and clavicular orientation was visually qualified from the x-rays, not quantitatively measured. The analyzed similarities to the human rhythm were inherent in the present methodology, as the human shoulder rhythm was used as the foundation of the creation of the chimpanzee shoulder rhythm. That the two were similar may be a reflection of the methodology, not commonalities between species. There is currently no manner of corroborating the present similarities in shoulder rhythm between species. Finally, the chimpanzee shoulder rhythm was derived using a very limited data set that included x-rays and bone scans from single chimpanzees, and

20 computed data points. The variability of the chimpanzee species, both in morphology, kinematics and full range of motion was not represented in this analysis. Therefore, the chimpanzee shoulder rhythm should be used cautiously. The primary purpose of deriving the chimpanzee shoulder rhythm was for implementation in a chimpanzee computational glenohumeral model. Though laden with assumptions, the method of derivation represents the best use of current, yet limited, available data for its specific purpose (Schmidt, 2005; Schmidt & Kraus, 2011). Should new data become available, the derivation can easily be expanded to strengthen the analysis and resulting chimpanzee shoulder rhythm.

4.4.5 Conclusion

While similar to humans, the chimpanzee shoulder rhythm derived in the present study had some differences that distinguish the species. Given the evolutionary and genetic closeness between chimpanzees and humans, it was plausible that they would exhibit similar shoulder rhythms. Differences existed that aligned with known structural and anatomical differences. Chimpanzees have resting scapular and clavicular positions that differ from humans due to their scapular shape and torso shape. The present data represents novel investigation into scapular and clavicular rotations in chimpanzees that demonstrates the likely existence of a shoulder rhythm in chimpanzees. However, the data set is very small, and should be verified with future studies.

4.5 Chimpanzee Glenohumeral Stability Ratios

Experimental studies have examined the multi-directional intrinsic stability of the human glenohumeral joint (Lippitt et al., 1993). Stability of the glenohumeral joint is complex and dependent on many physiological and biomechanical factors, but can be measured as a global quantity. One important measure of global intrinsic joint stability is the level of shear translational forces in the glenoid that can be applied along with a specific amount of compressive force before becoming destabilized (Figure 38B). This stability is intrinsically provided through the concavity of the glenoid, and can be represented as a ratio of shear to compressive force (Lippitt et al., 1993). The glenoid fossa is asymmetric in shape (Figure 38A). To understand the non-uniform stability of the joint, it is measured in multiple directions of superior, inferior, anterior and posterior, and 45° between each, for a total of 8 directions (Lippitt et al., 1993).

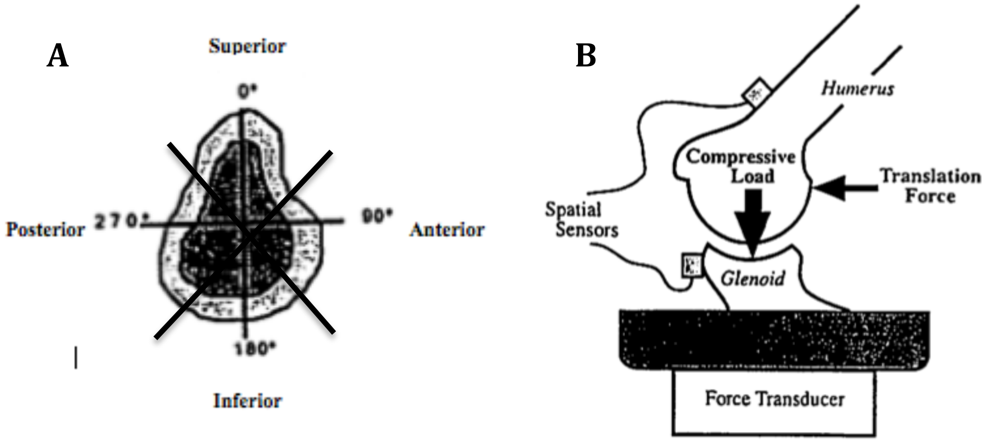


Figure 38: (A) View of the glenoid fossa, demonstrating the eight directions of stability testing of the joint. (B) Description of the setup for applying the shear, translational forces to determine the stability ratios. Shear forces were applied for a standardized compressive force directed into the joint center until dislocation occurred (from Lippitt et al., 1993).

Due to its asymmetry, the stability of the glenoid is not uniform in all directions. In the superior and inferior directions the glenoid depth is greater (Figure 39), and the joint requires greater shear forces to destabilize and dislocate (Lippitt et al., 1993). The fossa is wider superior to inferior, providing for greater depth (Figure 39).

Study of glenohumeral stability confirms its stability is proportional to its superior/inferior, and anterior/posterior shape, and depth (Lippitt et al., 1993).

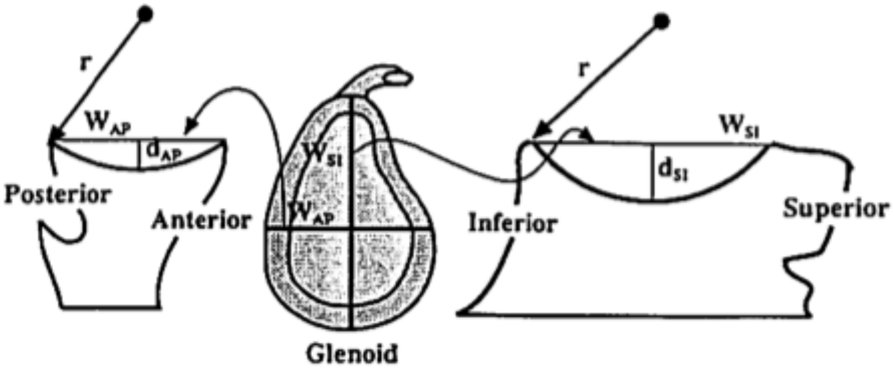


Figure 39: For the radius of curvature of the humeral head (r), the increased width of the glenoid fossa in the superior to inferior (W_{SI}) increases the glenoid depth (D_{SI}) compared to the anterior to posterior width (W_{AP}) and depth (D_{AP}) (from Lippitt et al., 1993).

4.5.1 Data Collection for Chimpanzee Stability Ratios

No data exists regarding stability ratios in the chimpanzee glenohumeral joint, but it is possible to infer the stability ratios of the chimpanzee glenohumeral joint using mechanical principles of stability and knowledge gained from human experimental studies. Differences between species in the factors that affect human stability ratios – glenoid fossa shape and depth – provide insight into how stability in chimpanzee and human glenohumeral joints likely differ.

Data on the chimpanzee glenoid morphology was obtained from literature sources. The traits compared included glenoid rim shape, glenoid superior/inferior width and anterior-posterior widths, concavity of the glenoid and glenoid depth (Larson, 1995; Larson, 2000; Macias & Churchill, 2015; Young, 2003; Young, 2004; Young, 2006; Young, 2008). Differences between humans and chimpanzees for each of these glenoid traits were determined. The differences between species in any of the glenoid shape and depth traits were used to apply commensurate proportional changes to the eight stability ratios for chimpanzees.

4.5.1.1 Differences in glenoid rim shape

Most primates share a similar glenoid shape. A principle component analysis on the geometric morphology of hominoid glenoid fossa examined both the shape and depth characteristics of the fossa between chimpanzees, humans, Neanderthals and orangutans using principle component analysis (Macias & Churchill, 2015). The superior-inferior elongation and anterior-posterior breadth principle component were not significantly different between humans and chimpanzees, but both differed from Neanderthals and orangutans (Macias & Churchill, 2015). Both chimpanzees and humans have a pear-shaped glenoid fossa (Figure 40).

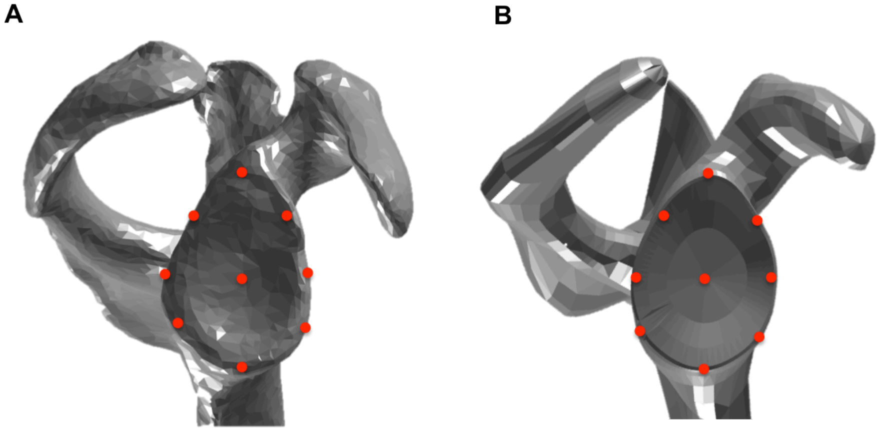


Figure 40: Comparison of the shape and centroid of the glenoid between chimpanzees (A) and humans (B). Both images are reproduced from medical imaging; the chimpanzee scan was of higher resolution. The outer rim shape is identified at every stability ratio angle, and the deepest point of the glenoid is also indicated.

4.5.1.2 Differences in glenoid width

Extant hominoids have been noted to share a wide glenoid fossa relative to other primate relatives (Ciochon, 1983). While this trait has been given anthropological significance, it may not be a very distinctive or functionally relevant trait (Larson, 1998). Glenoid height and width has been examined in a couple cross-species comparative studies of scapular shape. These studies typically examine multiple inter-related primate species, including humans and chimpanzees. In all such studies, the height of the glenoid, and the width of the glenoid were similar between chimpanzees and humans (Larson, 1995, 1998; Macias & Churchill, 2015; Young, 2003). Both have a glenoid that is approximately two-thirds wide as the fossa is tall (Larson, 1995; Macias & Churchill, 2015).

4.5.1.3 Differences in glenoid depth

Chimpanzee and humans are both deepest at the center of the glenoid, unlike their relative the orangutan that is deepest at a more posterior region (Macias & Churchill, 2015). This is likely related to the similar superior-inferior and anterior-posterior curvature profile between chimpanzees and humans, which has been shown to be not statistically different (Macias & Churchill, 2015).

Research on differences between humans and chimpanzees has demonstrated large similarities in both rim shape and direction-specific curve characteristics (Macias & Churchill, 2015). As differences in the glenoid shape appear to be negligible between species, it can be assumed that each of the human stability ratios can be altered by a constant multiplier that represents a ratio of the difference in depth between the two species.

4.5.2 Chimpanzee Stability Ratios Data Analysis

No statistical differences have been found between chimpanzees and humans in glenoid shape, width, height, or position of maximal depth. Therefore, the difference between species can be assumed to be the same in all stability ratio directions. A single multiplier can be applied to all directional human stability ratios, representing the relative difference in maximum depth of the glenoid fossa between species.

To determine differences in depth, measurements were taken on both the human and chimpanzee scapular bone scans. The two scans were scaled to have a glenoid of the same height. Three three-dimensional points were identified on both the human and chimpanzee glenoid – the most superior point and most inferior point of the rim, and the center of the glenoid. With scaled glenoid fossae, the midpoint of a line connecting the superior and inferior point was determined, and the distance from that point to the center point was calculated. The difference in this distance between the chimpanzee and human represented the ratio of difference in glenoid depth between the two species. The chimpanzee glenoid was approximately 25% deeper than the human glenoid.

To apply the difference in depth to the chimpanzee stability ratios, it had to be converted to millimeters. According to Matsen and colleagues (1994), stability ratios increase 10.9% for every 1mm increase in depth. No data exists on the average depth, in mm, of the chimpanzee glenoid fossa. However, data on the average human depth is available (Lippitt et al., 1993). Combined with the ratio of chimpanzee-to-human depth derived, this data was used to calculate the difference between species in millimeters. As the stability ratios are meant to be a global representation of all the intrinsic factors that contribute to glenohumeral stability ratios, the human glenoid depth used to derive the chimpanzee depth included the labrum (Matsen et al., 1994; Lugo et al., 2008; Veeger & van der Helm, 2007).

Though no data is available on the variability of chimpanzee glenoid depth, there is variability data available on glenoid height and width (Larson, 1995). This variability was extended to the glenoid depth to inform a statistical analysis of between species differences in glenoid depth. A t-test was run to determine if the differences between species were significantly different at $\alpha=0.05$.

4.5.3 Chimpanzee Stability Ratios

Chimpanzees were determined to have a glenoid that is 1.205mm deeper than humans. Compared to the human depth, inclusive of the labrum, of 4.8mm, chimpanzees have a glenoid that is 6mm deep. This translated into a 13.13% increase in stability in each direction (Matsen et al., 1994).

The glenoid fossa depth was not statistically significantly different between the two species (Table 10).

Table 10: Comparison of the glenoid fossa depth between species, with standard deviation in parentheses.

Depth Chimpanzee	Human	p-value
6.0048 (1.59)	4.8 (1.0)	0.174

4.5.4 Discussion

Objective two was met with the calculation of an additive factor to determine intrinsic chimpanzee stability ratios. Chimpanzees have a deeper glenoid than humans. However, this difference in depth was not significantly different.

The deeper chimpanzee glenoid fossa would theoretically provide more stability at the glenohumeral joint. The human glenoid is less stable than other joints in the body. The glenoid is less deep, and does not form a cup around the glenohumeral joint. It also lacks ligamentous support throughout the entire joint range of motion (Matsen et al., 1994; Veeger & van der Helm, 2007). While this reduces stability, it improves mobility, which is necessary for typical upper extremity motion (Wood & Richmond, 2000). Chimpanzees carry out similar behaviors and motions as humans. However, they also conduct weight-bearing locomotion with their upper extremity, which requires increased stability to counter large joint reaction forces (Lippitt et al., 1993). These behaviors include quadrupedal terrestrial knuckle-walking and arborealism in the form of quadrupedalism and bimanual climbing (Cartmill & Smith, 2009). The inclusion of weight-bearing locomotion is likely the reason for a deeper glenoid fossa. The increased depth provides a moderate increase in intrinsic stability to the joint, allowing the joint to incur larger shear forces (Matsen et al., 1994; Wood & Richmond, 2000).

There was no significant difference in glenoid fossa depth between humans and chimpanzees. Chimpanzees require greater stability at the glenohumeral joint for the purposes of locomotion (Wood & Richmond, 2000). Chimpanzees are not locomotor specialists, as they require their upper extremity for a variety of locomotor and daily living tasks throughout a wide range of motion in all three anatomical planes (Ashton & Oxnard, 1976; Doran, 1996). Therefore, they still require a large range of mobility at the glenohumeral joint to accommodate a large range of behaviors. A large increase in glenoid fossa depth would increase stability to the detriment of mobility (Matsen et al., 1994). The small increase in glenoid depth in chimpanzees likely represents a relative increase in stability proportional to the increase in weight-bearing activities that also preserves joint mobility.

It is possible that the chimpanzee glenohumeral joint has very different mechanisms of stability than humans, which were not accounted for in this investigation. There is no data available on chimpanzee glenohumeral ligament engagement. In humans, weight-bearing joints in the lower extremity have ligaments that are active throughout the range of motion (Matsen et al., 1994; Nigg & Herzog, 2007). That the chimpanzee glenohumeral joint is a weight-bearing joint may change ligamentous contributions compared to humans. However, these ligaments must allow for a wide range of behaviors and locomotor actions in chimpanzees (Cartmill & Smith, 2009). It is unlikely chimpanzee glenohumeral ligaments would behave as lower extremity ligaments. The chimpanzee glenohumeral joint likely has similar suction and adhesion mechanisms to improve stability as well. Chimpanzees may have increased intrinsic stability in the form of articular version. The superiorly orientated glenoid would provide a greater 'shelf' to contain the humerus than the laterally orientated human glenoid (Lugo et al., 2008). However this mechanism is most advantageous under gravitational loads. The glenohumeral joint experiences traction during brachiation behaviors, which would diminish the contribution of articular version of a superiorly oriented glenoid to joint stability. The increased intrinsic stability calculated here for chimpanzees is likely to be a conservative estimate, as it does not account for changes in other mechanisms of stability.

4.5.4.1 Limitations

The chimpanzee stability ratios were derived mostly from indirect analysis based on known morphological similarities between humans and chimpanzees, using previous published research. A direct analysis of the stability of the chimpanzee glenoid was not conducted in this study. It was assumed that the overall similar shape of the glenoid between humans and chimpanzees provided the rationale for using human stability ratios to derive chimpanzee stability ratios, based solely on differences in glenoid depth. Though relatively small, the human and chimpanzee glenoid do have differences in glenoid shape and concavity (Macias & Churchill, 2015; Voisin et al., 2006). These differences are likely rooted in the opposing primary functions of the glenohumeral joint between species. Intrinsic stability would be highly associated with the primary shoulder function. Therefore, small morphological differences in the glenoid that were not statistically significant in previous studies may have an effect on glenoid stability. These differences were not considered in the derivation of the stability ratios in the present study. Due to the weight-bearing usage of the upper extremity, the chimpanzee glenoid may also have greater inherent stability resulting from mechanisms beyond glenoid shape and depth (Veeger & van der Helm, 2007). This was not accounted for in the present study either, and has yet to be quantified. Finally, only a single chimpanzee bone scan was used in the analysis to quantify the difference in depth between species. This approach did not consider the variability in glenoid depth in chimpanzees. The derivation of the stability ratios, much like the shoulder rhythm, was done for the specific purpose of being utilized in a computational glenohumeral model. It represented a best approach with limited available data. Should more data become available, the glenoid stability ratios can be improved to better represent the true intrinsic stability of the chimpanzee glenohumeral joint.

4.5.5 Conclusions

Chimpanzees have greater depth of the glenoid fossa than humans. While it is not statistically significantly deeper, the depth of the chimpanzee glenoid fossa would generate increased intrinsic stability in the glenohumeral joint. Combined with greater articular version, the increases to intrinsic stability of the chimpanzee glenoid fossa represent a necessary tradeoff of increased stability without highly compromised joint mobility. This accommodates the wide range of motion required of chimpanzees to perform both arboreal and terrestrial weight-bearing locomotion.

Chapter 5 Study 3: Development of a Chimpanzee Musculoskeletal Glenohumeral Model

5.1 Introduction

Studies of evolution and biomechanics have typically fallen into three categories – comparative, experimental and modeling (Pontzer et al., 2009). For evolutionary science, comparative morphometric assessment has long been seen as the only available means to quantify the physical abilities and locomotion of human relatives and ancestors. This has usually involved comparisons of single skeletal features, or a series of skeletal features from fossils for association of form with function with extant hominids such as humans and the great apes (Young, 2008). Experimental studies have built upon morphometric analysis, typically comparing human behaviors and locomotion with those of the great apes. Experimental research has quantified differences between species in locomotor behavior, and provided clues as to probable adaptions following divergence from a common ancestor. There are difficulties with both these methods, however. Although bone shape has been linked to function (Oxnard, 1969) its specific dependency on function, locomotor behaviors, and specifically, biomechanics is difficult to quantify and assess (Young, 2005). The individual plasticity of skeletal features, and the effect of external stimuli in altering morphological features reduce the correlation between genetic and morphological phylogenetic assessments (Collard & Wood, 2000). Experimental work, while highly valuable, has been limited by subject availability and compliance, and procedural modifications for non-human subjects that reduce data precision and generalizability (Stevens & Carlson, 2008).

With the advent of sophisticated computational technology, modeling has only recently been employed. Modeling allows simulation of human, chimpanzee and even extinct hominin physical behaviors through integration of musculoskeletal information (O'Neill et al., 2014). Musculoskeletal models present an attractive prospect for advancement in the field of physical anthropology. This method integrates the effect of all musculoskeletal features at a joint or joints and enables comprehensive analysis of multiple physical behaviors. Further, the adaptability of the musculoskeletal parameters of these models creates a platform to test how changes to musculoskeletal morphology can potentially affect physical ability. Indeed, models have provided an opportunity for great insight into human evolution and human ability.

Musculoskeletal models demonstrate a new approach to understanding evolutionary biomechanics through interspecies comparisons. To date, no anthropological studies employing a musculoskeletal model have considered the upper extremity kinematics and kinetics of the human evolutionary path and the evolutionary holdovers defining modern human musculoskeletal shoulder capacity. As the closest living relative to humans, and a brachiating primate, a chimpanzee shoulder model that parallels the human Shoulder Loading Analysis Modules (SLAM) (Dickerson et al., 2007) could provide novel insights into the history of human arborealism and its relation to the form of the present human shoulder. A common persistent issue in physical anthropology concerns the definition of the physicality of an ape-like or human-like shoulder (Larson, 1995; Young et al., 2015). A prerequisite for creating musculoskeletal models of extinct hominins is creating one that represents both human ability and closely related “ape” ability. Chimpanzees represent the closest living relative to humans with a hybrid upper extremity utilized in arboreal and terrestrial locomotion and non-locomotor behaviors (Cartmill & Smith, 2009). Musculoskeletal models can provide the foundation for comparison between humans and chimpanzees in a variety of scenarios. The bookends of human and chimpanzee musculoskeletal shoulder models will aid in determining what morphological features distinguish these species. Eventually, this can inform where extinct hominin species fit on the continuum of ape-like arboreal and terrestrial, and human-like bipedal behaviors and capabilities, based on morphological features examined in fossil remains. And most critically for contemporary society, it will provide insights into the evolutionary form and function relationship of the modern human shoulder as it relates to specific musculoskeletal issues such as injury risk in overhead postures.

5.2 Purpose

The purpose of this study is to develop a model of the chimpanzee shoulder that parallels the human Shoulder Loading and Assessment Model created by Dickerson and colleagues (2007). The model will be evaluated using kinematic and electromyographical data on chimpanzees from the Stony Brook Primate Locomotion Laboratory (Larson & Stern, 1986; Larson et al., 1991; Larson, unpublished data). The kinematic, kinetic and muscular outputs of this model will be compared to those from the existing human shoulder model in an attempt to better delineate those musculoskeletal features that inhibit human performance of overhead behaviors. The model creation is outlined in Figure 41.

5.3 Hypotheses

Two primary hypothesis relate to anticipated output differences between the chimpanzee and human models:

Hypothesis one – Due to the relatively reduced force producing capacity of the shoulder musculature, humans will necessarily use the shoulder musculature at a higher normalized percentage of their maximum during simulated horizontal bimanual arm suspensory climbing. Further, humans will thus demonstrate a greater normalized total muscle effort than chimpanzees.

Hypothesis two – As a result of morphological and orientation differences of the scapula, chimpanzees will have a greater subacromial space in all climbing static instance postures.

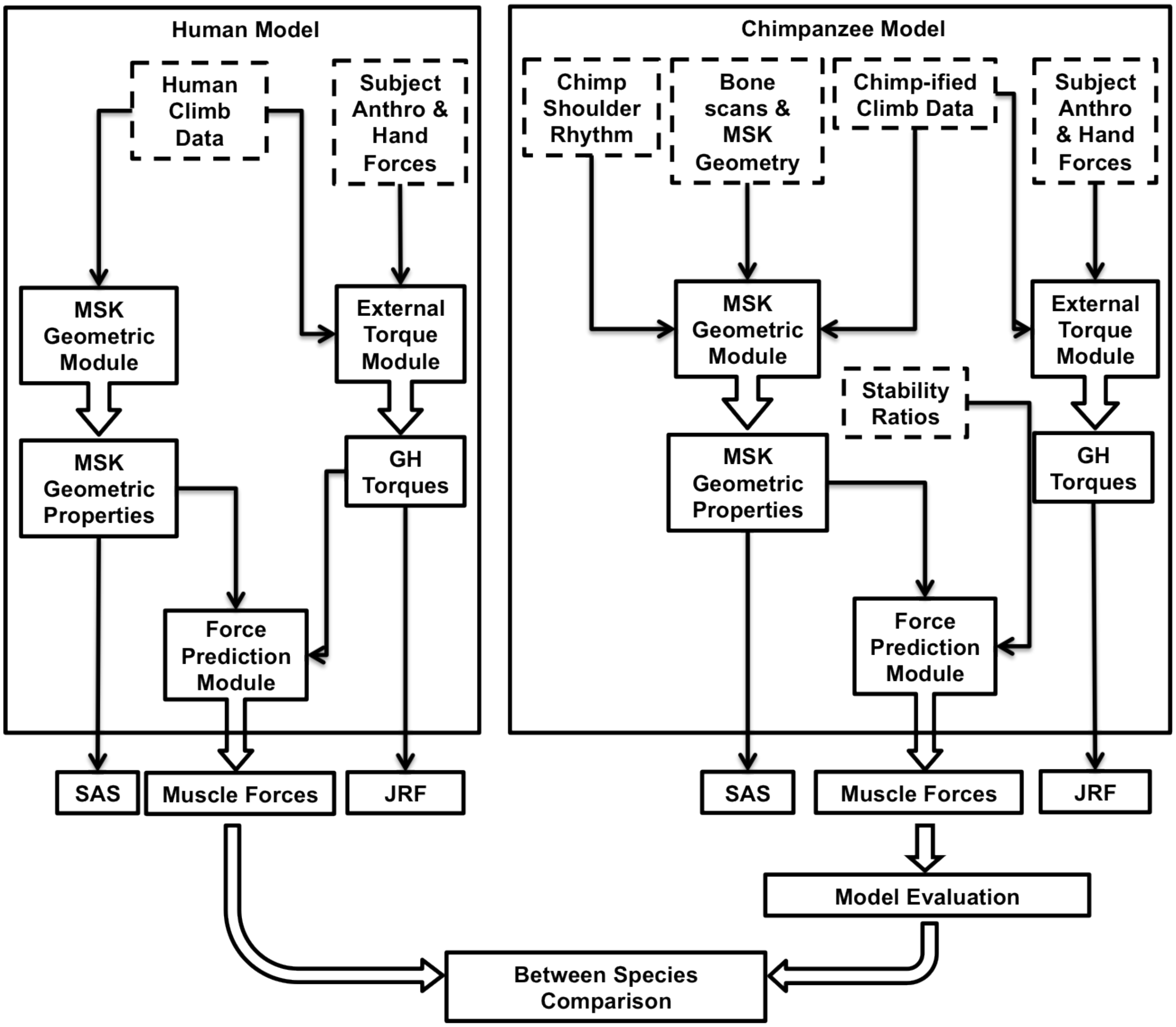


Figure 41: Outline of the steps for running the human model, development of the deterministic chimpanzee model and comparison of outputs between species. GH = glenohumeral; MSK = musculoskeletal; SAS = subacromial space; JRF = joint reaction forces. Model inputs are outlined in dashed boxes, model modules in black boxes and model outputs appear outside the model boxes. Specific outputs from the three modules are used for the comparison of model outputs between species.

5.4 Methods

This study required assembling a novel chimpanzee glenohumeral musculoskeletal model of the right arm, using the template of the extant human SLAM model (Figure 42). Part of the required data to achieve the new model was created by previous studies in this dissertation. The climbing motion capture data generated in Study 1 was converted into species-specific files to serve as the kinematic postural inputs for both the human and chimpanzee models external dynamic torque module. The chimpanzee shoulder rhythm generated in Study 2 was used as part of the Geometric Module of the chimpanzee model. Finally, the chimpanzee glenohumeral stability ratios also calculated in Study 2 were used as geometric constraints in the Force Prediction Module of the chimpanzee model (Figure 42).

Using SLAM as a template, the chimpanzee glenohumeral model was developed mostly through species-specific modifications to the geometric properties module. Scans of chimpanzee bones were provided through collaborators at the University of Massachusetts, Amherst and the University of Arizona. Other geometric data required for creating the chimpanzee model was sourced from literature. Comparisons of the physical function between the novel chimpanzee model and existing human model in the present study were made to infer musculoskeletal differences between human and chimpanzee physical shoulder abilities and limits.

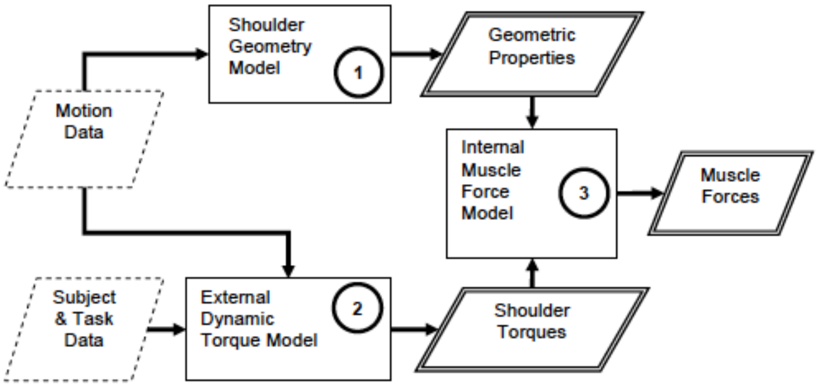


Figure 42: General template of the inputs, modules and outputs that define the original human SLAM model. Inputs are in dashed boxes, modules in black lined boxes and outputs are double-lined boxes. The overall structure was followed for the chimpanzee module, with chimpanzee-specific inputs and module parameters. Most differences between models occurred in the Geometric Properties module.

5.4.1 Development of Chimpanzee Glenohumeral Model

The model is comprised of three parts developed in Matlab® software: a musculoskeletal geometric properties module, an external dynamic joint moment module and an internal muscle force prediction module (Figure 42) (Dickerson et al., 2007).

The task analyzed in this study was:

1. A single overhead horizontal bimanual arm suspension climb cycle

This task was chosen, as it is widely considered common ancestral behavior in both species that is completed with very different levels of capability in modern chimpanzees and humans. Chimpanzees still habitually climb, while humans appear to no longer have a weight-bearing upper extremity suitable for locomotive purposes (Wood & Richmond, 2001).

The model was used to assess six different static instances of the climb cycle:

1. Early right support – double support phase
2. Mid right support – left swing, single support phase
3. Terminal right support – double support phase
4. Early right swing – down phase of arm swing
5. Mid swing – beginning of reach phase of arm swing
6. Terminal swing – pre-contact with support rung

These six instances all represent distinct time points of the climb cycle that require different levels of muscular support to stabilize the body and upper extremity (Larson & Stern Jr, 1986; Larson et al., 1991).

5.4.1.1 Glenohumeral Geometry Module

The geometry module is driven by subject specific morphological data, using bone scans and postural motion coordinate data as inputs to determine boney orientations and positions of each segment, and subsequent lines of action and moment arms for each of the muscle elements (Dickerson et al., 2007). There are five different parts of this module. The first is a segment parameter definition. The model has five segments – the torso, and the right side clavicle, scapula, humerus, and forearm. The dimensions of each of the segments were determined from existing data on average bone dimensions in the chimpanzee upper extremity (Larson, 1998; Schoonaert et al., 2007; Thorpe et al., 1999; Young, 2003). The second part is an algorithm for the shoulder rhythm. The mathematical representation of the chimpanzee shoulder rhythm was developed in Study 2. The shoulder rhythm determines scapular and clavicular rotations from thoracohumeral rotations, and is characterized by a total of six equations representing three clavicular rotations and three scapular rotations (Equations 7-12). These equations were incorporated into the model and used to define the orientation of the scapula and clavicle with respect to the humerus and torso.

The third and fourth parts of the geometry module are the definition of right-side muscles and muscle lines of action. Fourteen separate upper extremity muscles were modeled. Four of these muscles – biceps, triceps, infraspinatus, supraspinatus – were modeled with multiple mechanical elements to represent their multiple attachments for a total of 20 muscle elements. Chimpanzees share most of the same muscular anatomy as humans. The exception is chimpanzees have an additional muscle, dorsoepitrochlearis (Ashton & Oxnard, 1963; Diogo et al., 2013; Swindler & Wood, 1973). The dorsoepitrochlearis muscle typically arises from the latissimus dorsi or coracoid process and attaches on the distal humerus (Ashton & Oxnard, 1963). Muscle attachment sites were determined using published data (Ashton & Oxnard, 1963; Ashton et al., 1976; Carlson, 2006; Diogo et al., 2013; Swindler & Wood, 1973; Thorpe et al., 1999). Precise three-dimensional locations were not available for chimpanzee muscle origins and insertions. Estimations were made iteratively following muscle footprints provided in literature sources (Swindler & Wood, 1973). Muscle lines-of-action were modeled using spherical and cylindrical geometric muscle wrapping techniques that generate more physiologically representative lines-of-action about the glenohumeral joint (Dickerson et al., 2007; van der Helm, 1994). Finally, the fifth part of the module created contact force application sites between the scapula and ribcage, as well as ligament placements. Ligaments were set as inactive in both models.

The postural motion data inputs for the chimpanzee model geometric module were derived from the human motion capture files collected in Study 1. Data currently exists of chimpanzees and related primates performing brachiation tasks, including horizontal bimanual arm suspensory climbing (Demes et al., 2009; Reghem et al., 2013; Stern & Larson, 2001; Usherwood et al., 2003). Unfortunately, this data is not quantitative or three-dimensional, and is insufficient as kinematic inputs into the musculoskeletal model. A two-dimensional analysis in Study 2 demonstrated that humans and chimpanzees exhibit statistically similar two-dimensional climbing kinematics. Based on these results, in the absence of three-dimensional chimpanzee kinematics, human climbing kinematics were used as a surrogate for chimpanzee climbing kinematics. The kinematic data of a single experienced climber was used.

Systematic modifications were made to the human kinematic postural data to more adequately represent chimpanzees. First, the lengths of the upper extremity segments were altered to match the proportions of chimpanzee limbs by shifting the position of the joint centers (Schoonaert et al., 2007). Second, the position of the glenohumeral joint was shifted to represent chimpanzee bone positions. Chimpanzees have a narrower ribcage superiorly, and a more superiorly oriented glenohumeral joint. X-rays of chimpanzee shoulders provided by the University of Stony Brook, New York, were used to guide the heuristic shift in position of entire upper extremity through movement of the humeral head and acromion markers to more medial and superior positions. Orientation and postures of the six static climbing instances were preserved through the joint position and arm length adjustments. Following these modifications, the Vicon motion capture data from the human climbing study was converted to a standardized file format that provides three-dimensional joint center and marker locations for model operation.

5.4.1.2 External Dynamic Torque Module

The external dynamic moment module uses motion capture data to derive external forces and moments using inverse dynamics (Dickerson et al., 2007). The moment module was driven by the same motion capture data inputs used to drive the geometric module.

The moment module has four steps. The first was the description of segment properties. Segment properties of the upper extremity (upper arm, forearm and hand) were determined using anthropometric data on segment masses, lengths and moments of inertia (Thorpe et al., 1999; Schoonaert et al., 2007; Zihlman et al., 1992). Modified human motion data was used to estimate the center of rotation for the glenohumeral, elbow and wrist joints, which were then used to determine locations of the segmental centers of mass (Dickerson et al., 2007). Local coordinate systems for each segment were then defined. The second and third parts of the module are the calculation of linear and angular kinematics. These were determined from differentiating filtered motion data and the Euler angle decomposition method employed by Vaughn and colleagues (1992) (Dickerson et al., 2007). These derivations allow the completion of the fourth step, which is calculation of external joint forces and net moments. Forces and moments were calculated using Newtonian laws of motion (Dickerson et al., 2007). Gravity was the only external force applied, with the reaction force acting at the hand. In swing phase of the climb cycle, this translated to an external force equivalent to the mass of the upper body segments. In the mid-support phase of the climb cycle, when only the right hand provided support, the external force acting at the hand was equivalent to total body mass. At early and late support, the external force was equally shared by both limbs and was half of body mass for the right hand.

5.4.1.3 Internal Muscle Force Prediction Module

The outputs of both the geometry and moment modules provide inputs to the force prediction module (Dickerson et al., 2007). The high number of muscles that contribute to glenohumeral motion make it an indeterminate system, with more muscles than mechanical equations to define the system (Dickerson et al., 2007). Thus an optimization approach was used to generate muscle force predictions using muscular and mechanical constraints. The optimization routine consists of five interconnected parts that delimit potential force prediction solutions, enhancing physiologic feasibility.

The first was a series of mechanical constraints for the three-dimensional angular and linear equilibrium of the glenohumeral joint, comprised of muscle forces, joint contact forces and external forces. An additional mechanical constraint was enforced for elbow joint flexion/extension moment equilibrium.

Second, muscle force bounds are created. The lower bound for all muscles was 0, while the upper bound was proportional to the absolute physiological cross-sectional area (PCSA) of each muscle, based on published data (Table 11) (Carlson et al., 2006; Kikuchi, 2010; Michilsens et al., 2009; Mathewson et al., 2014; Oishi et al., 2009; Thorpe et al., 1999; Ward et al., 2006), multiplied by a specific tension value. As no data exists for baseline muscle tension in chimpanzees, the previously used human, specific tension of 88N/cm^2 was applied to determine muscle force upper bounds (Wood et al., 1989). Where PCSA data did not exist for chimpanzees, the PCSA of closely related brachiators such as orangutans and gibbons was used and scaled by overall body mass to determine a mass appropriate physiological cross-sectional area of the muscle for chimpanzees.

Table 11: Muscle PCSA for all elements included in the force prediction module of the Human and Chimpanzee glenohumeral model. Absolute values are given, as well as relative to the total body mass of the human and chimpanzee individuals used in each model.

	Absolute PCSA (cm^2)		**Relative PCSA to Body Mass (cm^2/kg)**	
Muscle	**Human***	**Chimpanzee***	**Human***	**Chimpanzee ***
Dorsoepitrochlearis	n/a	2.98	n/a	0.066
Deltoid middle	7.42	28.95	0.103	0.643
Deltoid posterior	4.29	11.06	0.060	0.246
Deltoid anterior	8.84	12.10	0.123	0.269
Coracobrachialis	1.58	7.85	0.022	0.174
Infraspinatus 1 (upper)	6.37	11.08	0.088	0.246
Infraspinatus 2 (lower)	7.67	13.34	0.107	0.296
Subscapularis 1 (upper)	2.83	11.19	0.039	0.249
Subscapularis 2 (middle)	3.72	14.71	0.052	0.327
Subscapularis 3 (lower)	5.10	20.17	0.071	0.448
Supraspinatus	3.15	19.92	0.044	0.443
Teres major	8.48	12.69	0.118	0.282
Teres minor	2.81	5.48	0.039	0.122
Biceps (long)	4.94	10.10	0.069	0.224
Biceps (short)	2.18	8.06	0.030	0.179
Triceps (long head)	9.98	15.39	0.139	0.342
Triceps (medial head)	8.98	24.49	0.125	0.544
Triceps (lateral head)	8.98	17.09	0.125	0.380
Brachialis	9.98	20.43	0.139	0.454
Brachioradialis	2.00	8.52	0.028	0.189

* Human PCSA was acquired from Makhsous, 1999. The human data was measured from elderly individuals. As PCSA decreases with age, the values presented here have been doubled to more accurately represent the PCSA of younger, healthy human adults. Chimpanzee PCSA were acquired or derived from Carlson et al., 2006, Kikuchi, 2010, Michilsens et al., 2013, Oishi et al., 2009, and Thorpe et al., 1999.

The third constraint was a glenohumeral contact force. This used the glenohumeral stability force ratios determined in Study 2 to determine force thresholds in eight directions perpendicular to the surface of the glenoid (Dickerson et al., 2007).

The fourth part of the prediction module was the objective function of the optimization routine (Equation 13). This function weighs the muscle force prediction by the absolute physiological cross sectional area (PCSA) of that muscle and seeks to minimize the summation of the individual cubes of the muscle stresses.

It has been used in similar shoulder models and creates force sharing amongst agonistic muscles (Chaffin, 1997; Dickerson et al., 2007; Dul 1988). PCSA and muscle masses of chimpanzee upper extremity muscles were extracted from literature sources (Carlson, 2006; Kikuchi, 2010; Michilsens et al., 2009; Oishi et al., 2008; Oishi et al., 2009; Potau et al., 2009; Thorpe et al., 1999; Ward et al., 2006). The model solved for muscle forces, joint contact forces and torques, and directional dislocation force ratio coefficients (Dickerson et al., 2007).

Equation 13: Objective function used in the Force Prediction module to predict individual muscle forces. The objective function represents the summation of the individual cubes of the muscle stresses.

$$\Theta = \sum_{i=1}^{20} \left(\frac{f_i}{PCSA_i} \right)^3$$

5.4.2 Evaluation of the Chimpanzee Shoulder Model

The chimpanzee glenohumeral model was evaluated using a concordance analysis of experimentally collected EMG data and computational model muscle force predictions. Evaluation of the chimpanzee model presented challenges unfamiliar to human modeling efforts. As novel experimental data on chimpanzees cannot be readily acquired due to new legislation and lack of experimental facilities, model evaluation was limited to comparisons with previously published data on chimpanzee muscle activity. The tissue loading predicted by the chimpanzee model was assessed through comparison with published and unpublished experimentally acquired EMG data using concordance analysis (Dickerson et al., 2008). This analysis determines timing concordance in muscle activity and inactivity between EMG and predicted model muscle forces. If both the EMG and predicted muscle forces predict muscle activity above defined thresholds, there is concordance. If one indicates activity and the other does not, there is discordance (Dickerson, 2008). A concordance analysis is appropriate in this scenario, as instantaneous relative EMG amplitudes are highly variable with postures and movements, normalization methods, and typically show weak relationships with predicted muscle forces

(Makhsous, 1999; van der Helm, 1994). As little data exists that includes EMG of chimpanzees brachiating, this method also prevents biased evaluation of the predicted muscle forces via a limited EMG data set. The concordance analysis was used to assess each of the six static instances of the climb cycle described in 5.4.1, representing six static points of a full climb cycle of the right arm.

Studies that have analyzed muscle activity in primates have not conducted maximal voluntary contractions to normalize EMG produced during activity, as it is not logistically possible. EMG from primates is often normalized to the maximal EMG signal produced during the task of interest (Larson et al., 1991; Usherwood et al., 2003). To determine the "active" or "inactive" state of a muscle, a predicted model muscle force was considered "active" if it was greater than 5% of its maximal force producing capacity (Dickerson et al., 2008). Due to possible noise and spurious predictions, chimpanzee EMG signal was considered "active" if it was above approximately 5% of the maximal produced signal. Only select muscles were included in the concordance analysis, due to availability of experimental data. These included published data on anterior deltoid, middle deltoid, posterior deltoid, supraspinatus, infraspinatus, subscapularis, teres minor, triceps brachii, teres major and coracobrachialis (Larson, 1988; Larson et al., 1991; Larson & Stern, 1992; Larson & Stern, 2013). Unpublished data was also retrieved from University of Stony Brook, New York, courtesy of the Department of Anatomy and used in the concordance analysis. These muscles includes triceps brachii, coracobrachialis, and middle deltoid.

5.5 Data Analysis

Once the chimpanzee glenohumeral model development was complete, the model was run for evaluation analysis and for comparative analysis with the human glenohumeral model. Anthropometric, hand force and kinematic postural inputs for both models were applied for model operation, and selected deterministic outputs were compared between species.

5.5.1 Subject Anthropometric and Hand Force Inputs

Anthropometrics were used to approximate segment parameters for determining joint forces and moments in the external dynamic torque module. An approximately average healthy human male (mass: 72kg; height: 1.8m) and an average chimpanzee male (mass: 45kg; height: 1.32m) were used as the criteria subjects within each species-specific glenohumeral model.

Hand forces were dependent on the climbing phase, and were used in the external dynamic torque module to predict joint forces and moments. As the model was run statically, gravity was assumed to be the only external force, the reaction force of which acting at the hand. In the three static instances of support phase, two different hand forces were possible. Early and late support are double support phases, where both the right and left hand are in contact with support rungs. In these phase instances, mass was assumed to be distributed evenly between both support hands, and the hand force for the right hand was half of body mass (Figure 43). In mid support, the left arm is in swing phase and only the right arm provided support. The hand force in mid-support phasic instance was total body mass. In swing phase, the right arm provides no support. Therefore the external force acting at the hand was segment mass.

5.5.2 Postural Input Data

The motion data of a single male, experienced climber participant from Study 1 was used as postural inputs for both the human and chimpanzee glenohumeral models. This data was selected as it came from a male of average body mass and height, with kinematic waveforms that were very similar to the mean waveform. This motion data was modified to be more representative of the chimpanzee shoulder structure for the chimpanzee model.

The models produced six static time point data snapshots within a right arm horizontal bimanual arm-suspension climb cycle. The postures of these six phasic instances for both the chimp model and SLAM are shown in Figure 43. Both models used the same base kinematic inputs, but with systematic joint position and segment length modifications in the chimpanzee model. Hand and forearm lengths were altered, and the glenohumeral joint center and acromion data point (representing scapular position) were translated mediolaterally and superioinferiorly to reposition the shoulder to accurately represent chimpanzee shoulder position. Joint orientation was not altered. Therefore, both the chimp model and SLAM used the same overall static upper body postures as inputs (Figure 43). The arm is most horizontally adducted and extended forward in late swing and early support. In late support the arm is horizontally abducted and most elevated, and resultantly also positioned closest to the torso. Arm elevation decreases with the beginning of swing phase as the hand is released from the support rung and begins to horizontally adduct (Figure 43).

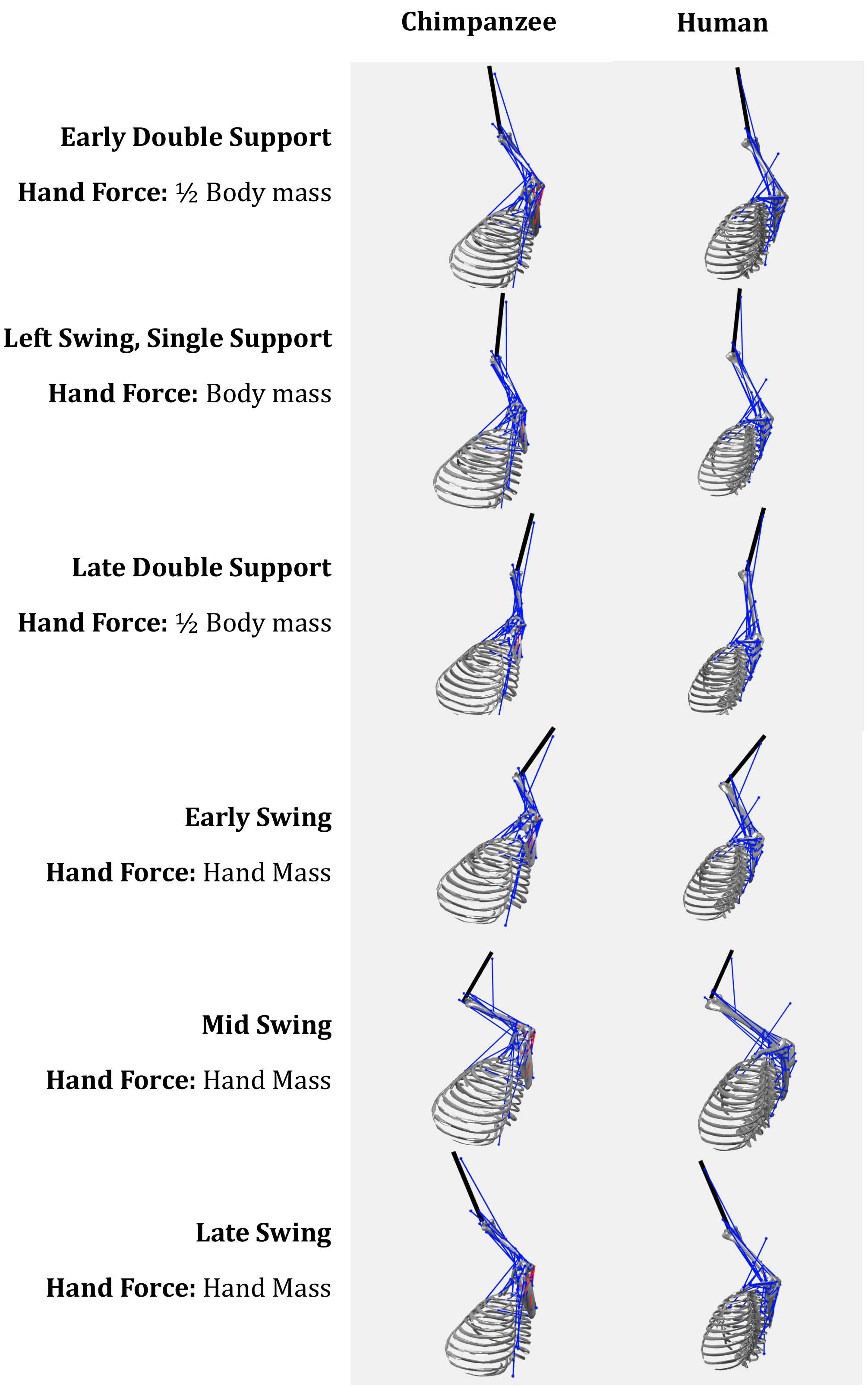


Figure 43: Postures for both the chimpanzee and human model in all six of the static phasic instances representing a full right arm climb cycle.

5.5.3 Between species comparison

Chimpanzee model outputs from the climbing task were compared to those produced by the human SLAM model while conducting the same functional task of horizontal bimanual arm suspensory climbing. The comparison between species was made for six static instances of a single right arm climb cycle. Using data collected in Study 1, the original SLAM was executed using experimentally measured climbing kinematics, subject anthropometrics and estimated external hand forces to determine resultant human glenohumeral musculoskeletal outputs. The chimpanzee model was subsequently executed using the geometrically modified human kinematics from Study 1 to determine subsequent chimpanzee glenohumeral musculoskeletal outputs.

Output dependent variables that were compared between human and chimpanzee models included local glenohumeral joint reaction forces and moments, individual muscle force and subacromial space. Muscle forces compared between humans and chimpanzees included the rotator cuff (supraspinatus, infraspinatus, subscapularis, teres minor), anterior deltoid, middle deltoid, posterior deltoid, teres major, biceps brachii, triceps brachii, coracobrachialis, brachialis, and brachioradialis. Local joint reaction forces were the global joint reaction forces rotated into the local body segments. As it is only extant in chimpanzees, analysis of the dorsoepitrochlearis muscle extended only to examination of muscle force sharing predictions in the chimpanzee model. A normalized total muscle force was also reported. All 19 or 20 normalized muscle forces from the human and chimpanzee model, respectively, were summed and divided by the total number of muscle elements observed in each phasic instance of the climb cycle. Subacromial space was the distance between inferior portion of the acromion and the most superior point of the humeral head.

Each model generated single values for each of the dependent variables for an average human and chimpanzee. This precluded the use of typical statistical analyses for determining significantly different differences between species in shoulder biomechanics. Differences between species were quantified and presented as an initial observation of differences between average chimpanzees and humans in shoulder function and physical capability. Chapter 6 explores systematically introducing variability into aspects of the biomechanical model to characterize the sensitivity of these outputs to various model parameters.

5.6 Results

5.6.1 Chimpanzee Model Evaluation

To evaluate the chimpanzee glenohumeral model, muscle force predictions were compared to chimpanzee experimental electromyographical muscle activations while performing the same task – horizontal bimanual arm suspension across all six static climb cycle instances. The static climb cycle instances represent discrete static points in the climb cycle where the electromyographical and muscle force prediction on/off status of each muscle was assessed. The electromyographical data was provided as descriptive and graphical data. This format did not allow for a quantitative, statistical concordance analysis. Instead, a qualitative concordance analysis was performed to determine the plausibility of the muscle force outputs of the chimpanzee glenohumeral model. Data on experimental muscle activity was converted to the graphical representation to allow comparisons with the static outputs of the chimpanzee model. The provided figure-based and written descriptive EMG muscle activity was qualitatively interpreted based on relative magnitudes to represent activity in each of the six static instances outputted from the chimpanzee model. Muscles that were modeled as multiple muscle elements – infraspinatus, subscapularis, and triceps brachii – were combined for the concordance analysis, as they were experimentally analyzed as a single muscle element.

The timing concordance comparison between model and experimental muscle activity outputs at discrete time points of the climb cycle demonstrate similarities between experimental and computational muscle activity. When both model and experimental data show activity, concordance is indicated (Figure 44). A total of 12 muscles with 6 discrete time points were used to determine concordance between predicted and observed muscle activity, for a total of 72 data points. Concordance occurred – both model and EMG predicting on or off – in 51 of 72 data points, or 70.8%. Concordance was apparent in all muscles. The lowest concordance was in subscapularis, posterior deltoid, and brachioradialis all of which had a concordance of 0.50 (Figure 44). Highest concordance of 1.0 was in infraspinatus and middle deltoid (Figure 44).

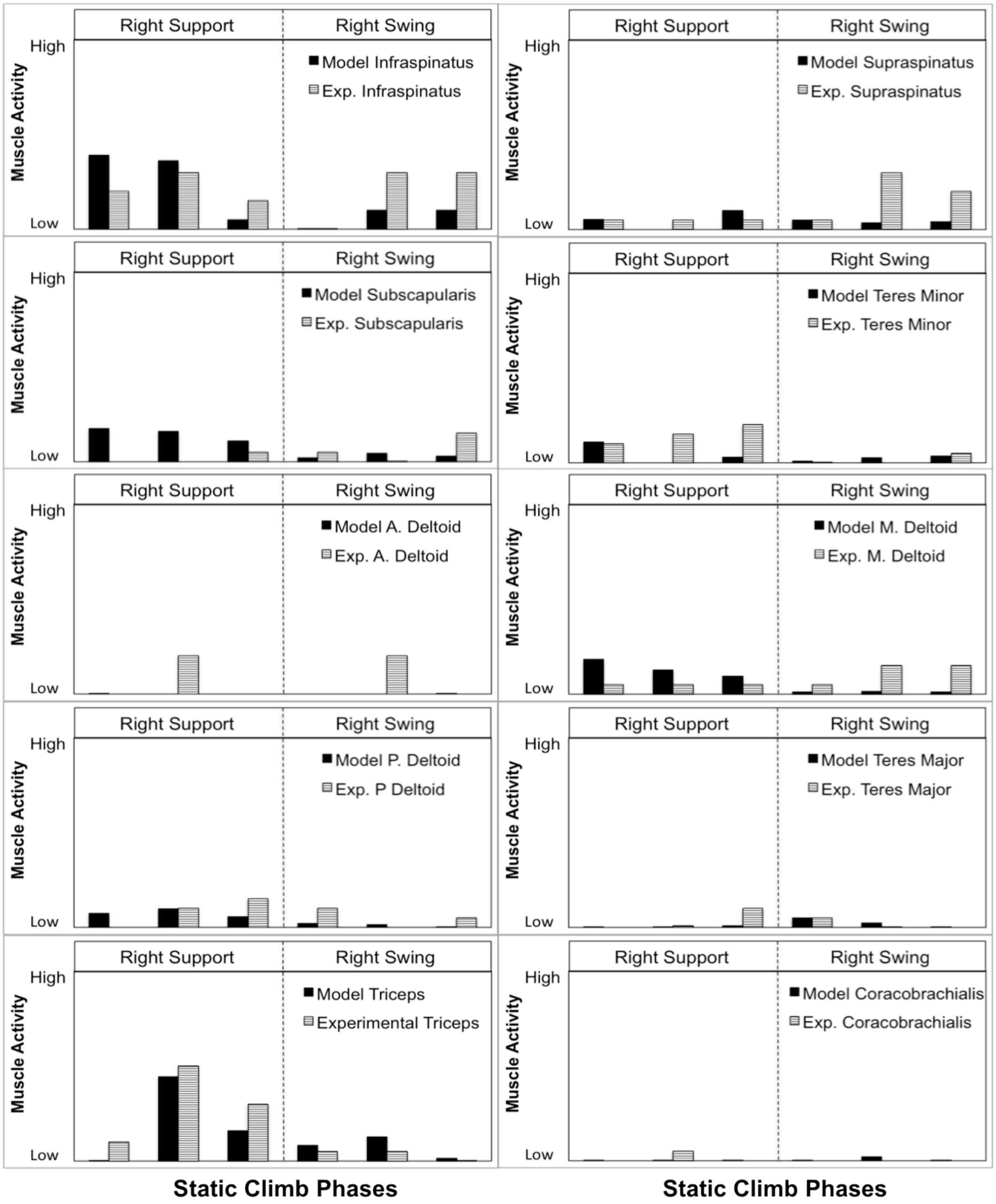


Figure 44: Discrete static on/off instances of predicted ("model") muscle activity versus experimental ("exp.") muscle activity for the same climbing activity. The support and swing phases each comprised of three distinct static points. While estimated experimental amplitudes are given, concordance was considered present only when muscle activity timing matched between the predicted and experimental results.

5.6.2 Predicted Joint Contact Forces and Torque

Joint reaction forces between species were compared by rotating the global joint reaction forces into the local glenohumeral system. As the same joint kinematics were used as inputs to both the human and chimpanzee glenohumeral models, differences in joint reaction forces and torques resulted from differences in body mass and segment mass, not climbing postures and techniques. The human glenohumeral joint was not only exposed to greater joint reaction forces, but also greater joint torques across all planes and axes, particularly during the right support phase (Figure 45 and 46).

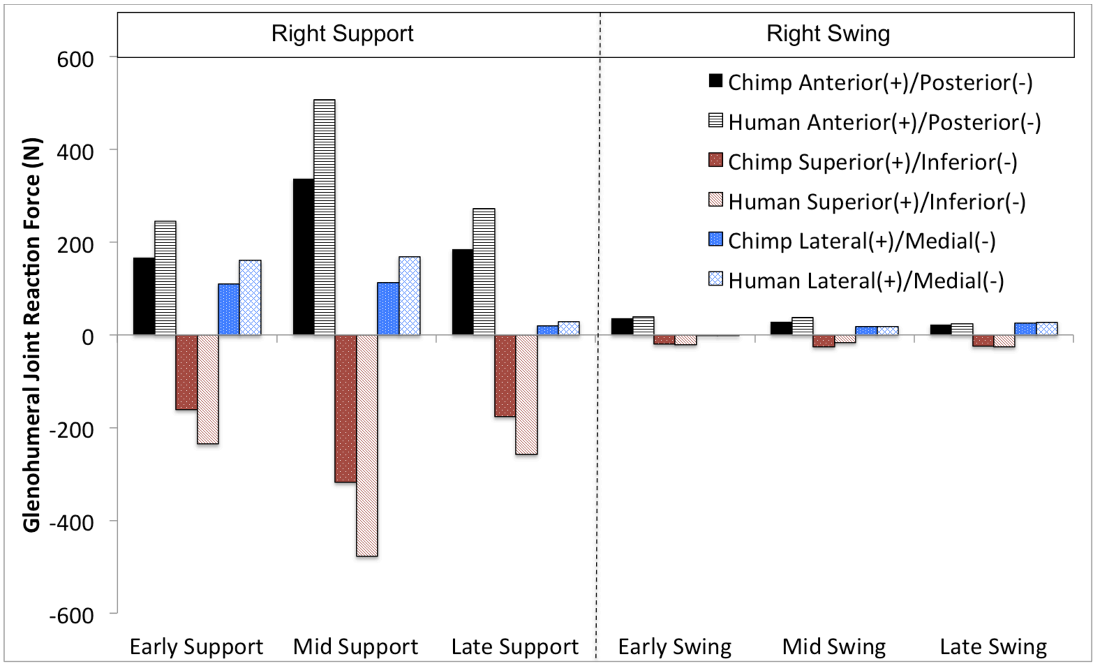


Figure 45: Predicted chimpanzee and human glenohumeral joint reaction forces for a single right arm climb cycle.

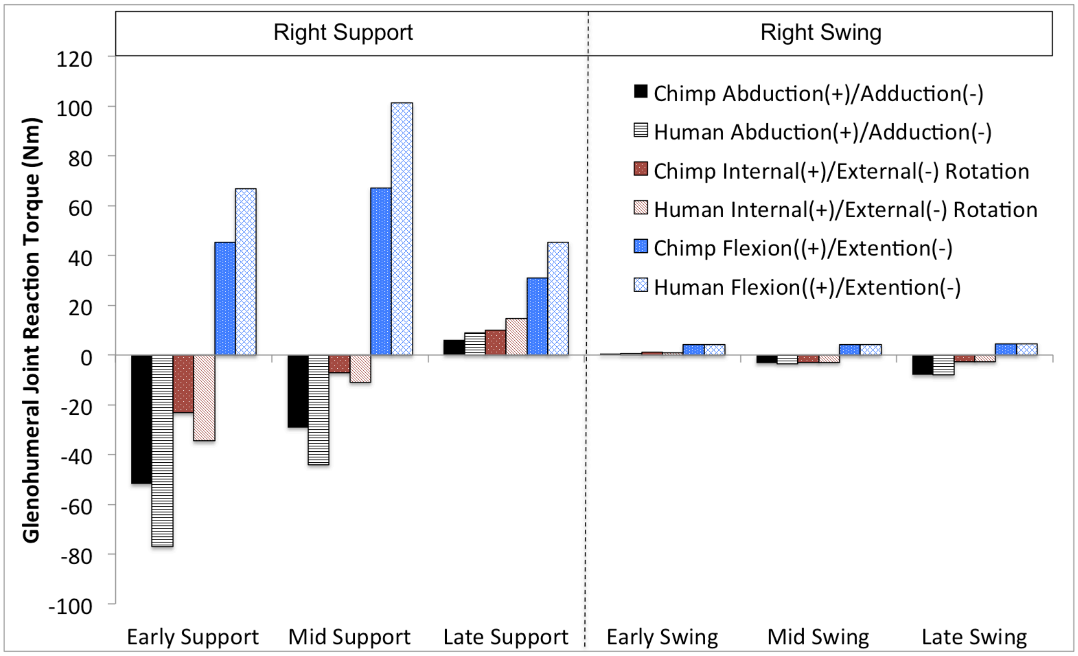


Figure 46: Predicted chimpanzee and human glenohumeral joint torques for a single right arm climb cycle.

5.6.3 Predicted Muscle Forces

Predicted rotator cuff muscle forces derived from both the chimpanzee and human glenohumeral models showed large differences between species. The infraspinatus and teres minor were predicted to contribute greater force in humans than chimpanzees in support phase, whereas activity in supraspinatus and subscapularis muscle forces were marginally greater in chimpanzees than humans in support phase (Figure 47). The human infraspinatus lower muscle element was recruited to maximal force and teres minor to nearly maximal force in early support (Figure 47). The human model predicted no supraspinatus and very low late support phase subscapularis contribution to support phase in humans (Figure 47).

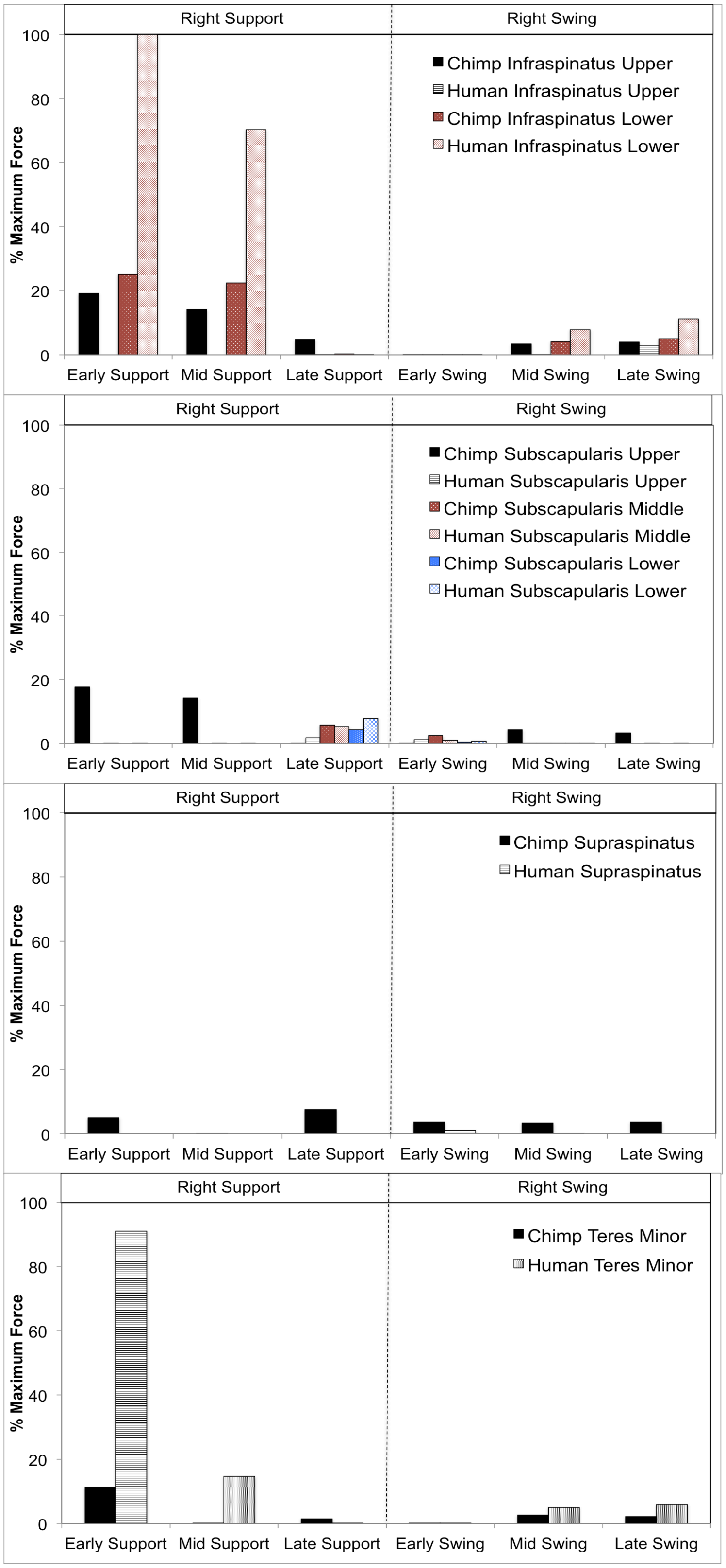


Figure 47: Predicted chimpanzee and human rotator cuff musculature recruitment, as a percentage of maximum force producing capability, for a single right arm climb cycle.

Humans were predicted to have greater muscle force contributions from all portions of the deltoid than chimpanzees in support phase (Figure 48). The deltoids were largely inactive in both species in the swing phase, with low force increases occurring in the late swing phase instance when the arm is raised to the next support rung (Figure 48). Anterior deltoid was predicted to not contribute to the climbing task in either support or swing phase in the chimpanzee model.

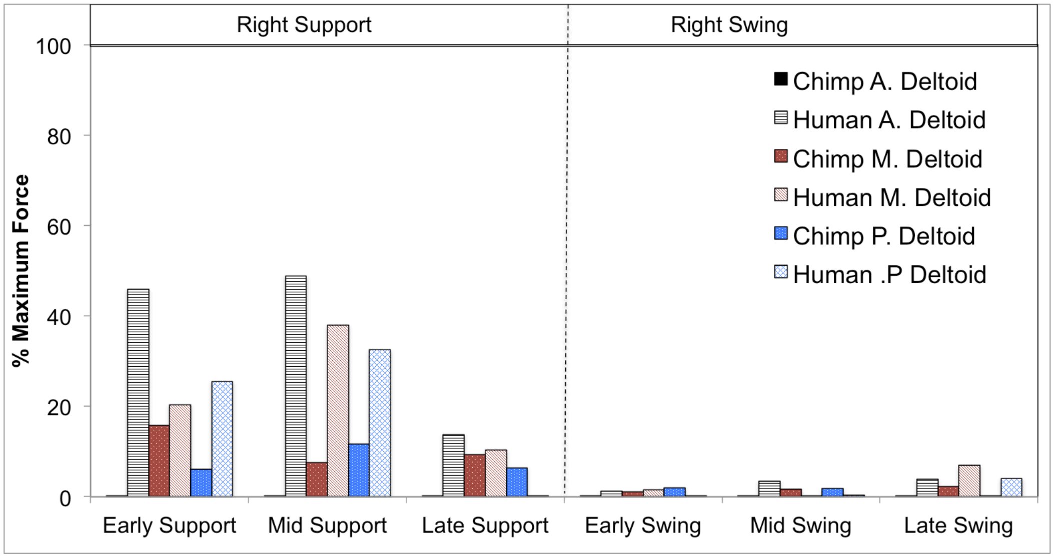


Figure 48: Predicted chimpanzee and human recruitment of the deltoids, as a percentage of maximum force producing capability, for a single right arm climb cycle.

Teres major, coracobrachialis and dorsoepitrochlearis were limited contributors to completing the climbing task. Dorsoepitrochlearis is only present in chimpanzees and was active in early to mid-support (Figure 49). Only in the human simulation was coracobrachialis predicted to contribute to the glenohumeral joint equilibrium in early swing and minimally in late swing (Figure 49). Teres major was marginally active in early to mid swing in chimpanzees (Figure 49).

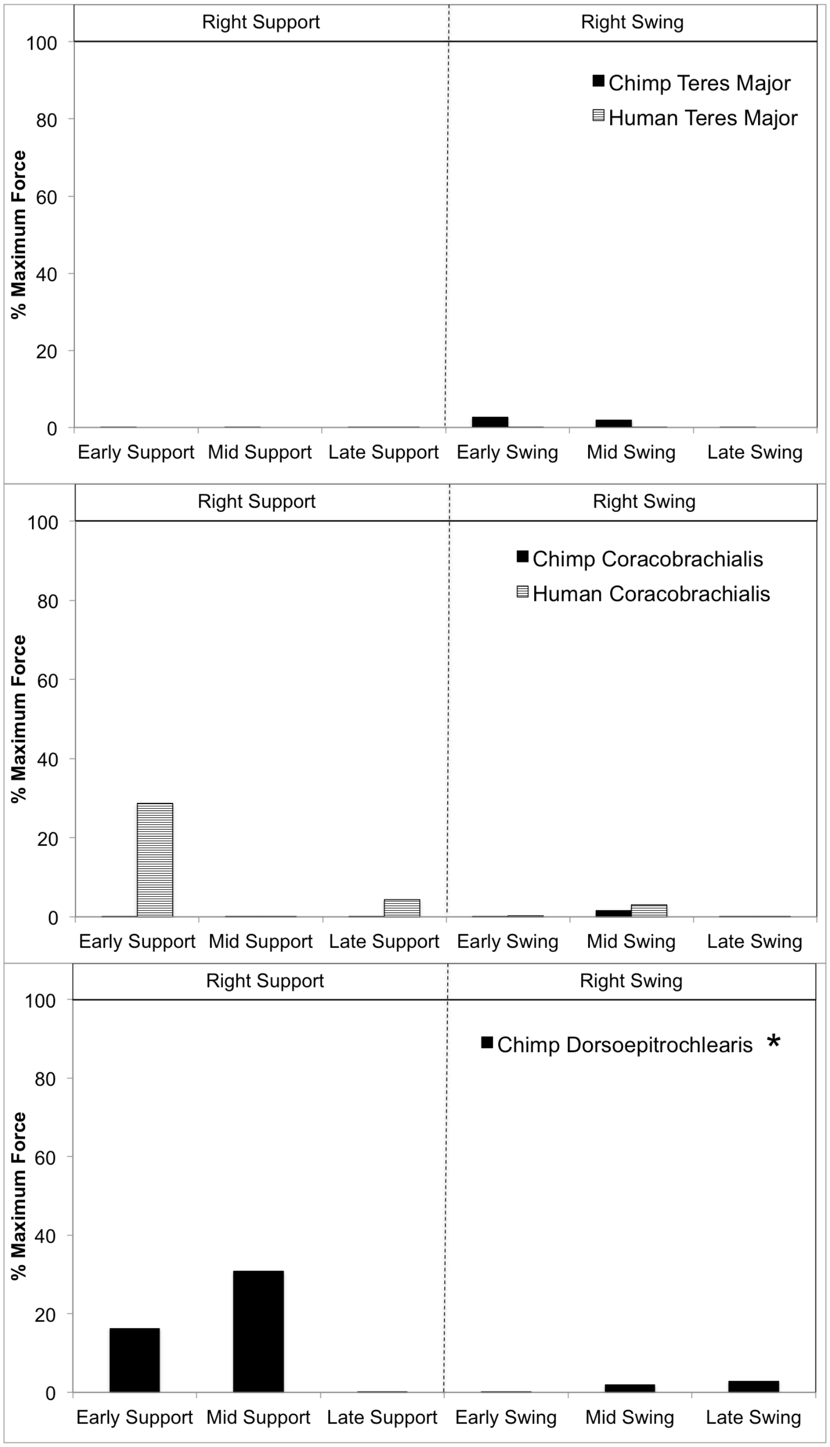


Figure 49: Predicted chimpanzee and human recruitment of the glenohumeral joint muscles of teres major, coracobrachialis and dorsoepitrochlearis as a percentage of maximum force producing capability, for a single right arm climb cycle. * Dorsoepitrochlearis is only present in chimpanzees.

As multi-joint muscles, the triceps and biceps contributed to climbing at the elbow and glenohumeral joint. The triceps long head and lateral heads were active in chimpanzees during left swing, which was a single support phase (Figure 50). Humans were predicted to activate the triceps medial head in early to mid support, whereas the triceps long head was the greatest contributor to the glenohumeral and elbow joint force in the human model (Figure 50). The bicep was more active in the human model, contributing a very high percentage of maximal force in early and mid-swing, with only minor activity in early support and late swing predicted in the chimpanzee model (Figure 50). Neither muscle was predicted to contribute significantly to swing phase.

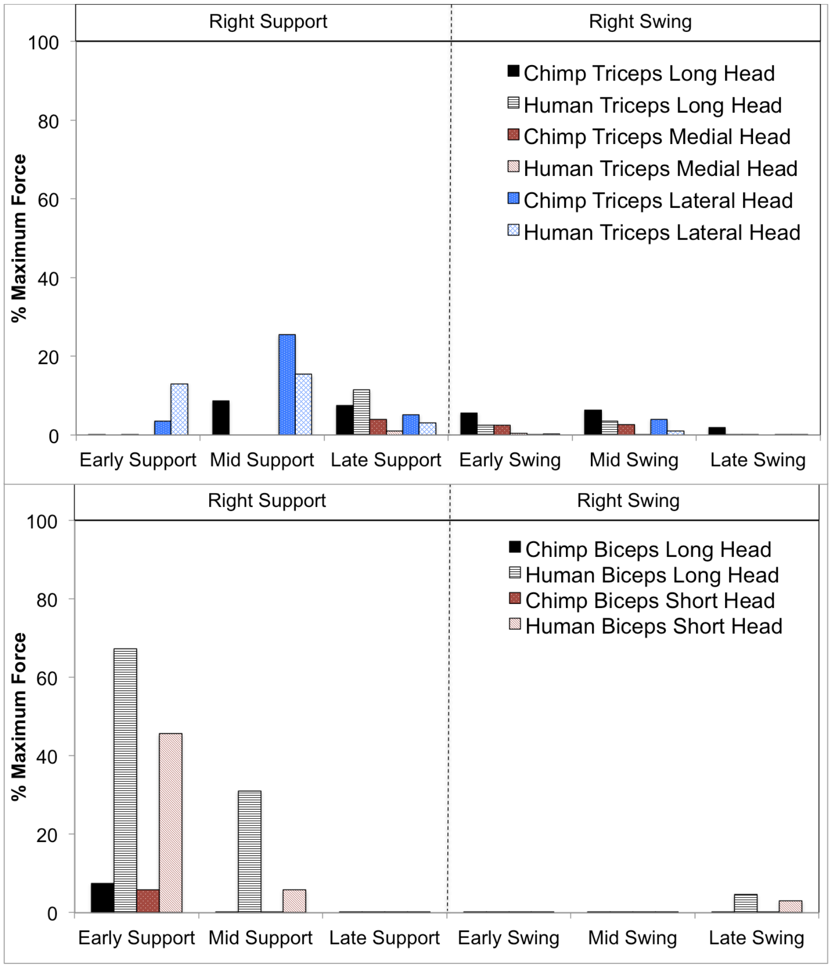


Figure 50: Predicted chimpanzee and human recruitment of the multi-joint triceps brachii, biceps brachii as a percentage of maximum force producing capability, for a single right arm climb cycle.

At the elbow, along with the biceps, humans were predicted to rely mostly on brachioradialis, with muscle force contributions as high as 70% of maximum force production capability (Figure 50 and 51). Chimpanzees utilized brachialis more than humans in mid-support. Chimpanzee brachioradialis was recruited at a much lower muscle force than humans during support phase.

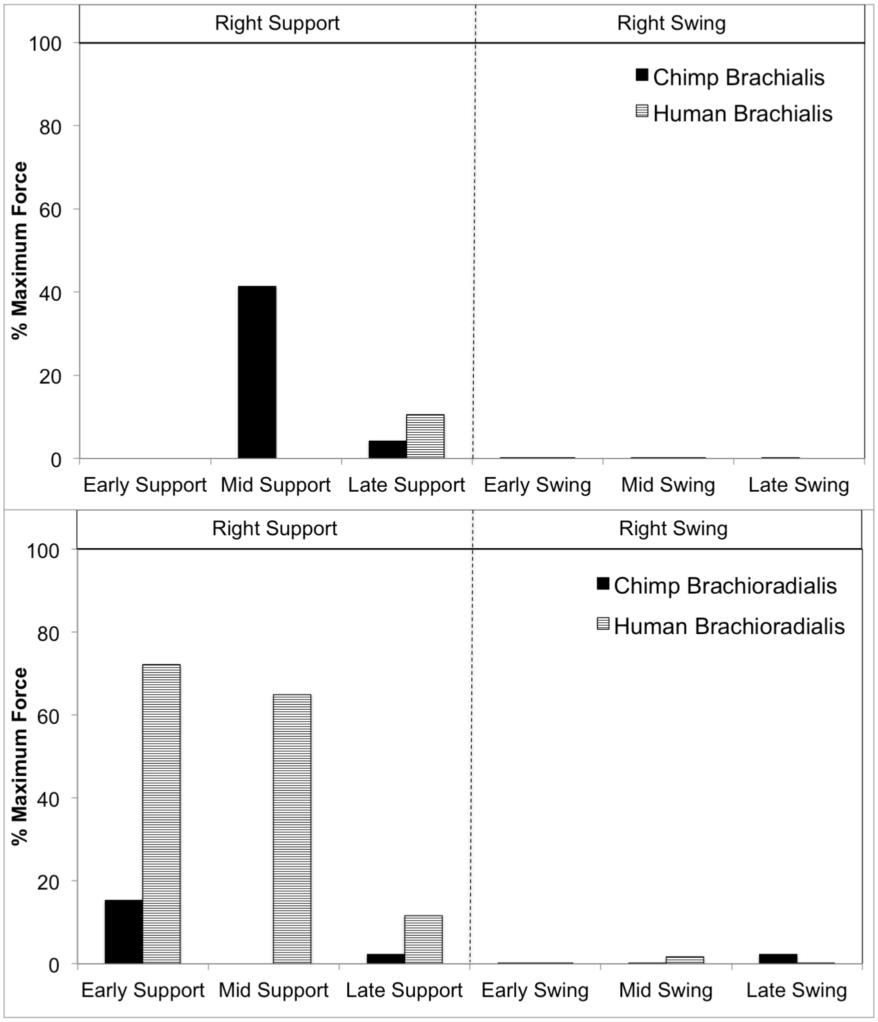


Figure 51: Predicted chimpanzee and human single-joint elbow musculature recruitment of brachialis and brachioradialis, as a percentage of maximum force producing capability, for a single right arm climb cycle.

Normalized total muscle force was much higher in the human model than the chimpanzee model during support phase (Table 12). Normalized total muscle force was predicted to be more than three times as great in humans in early support. The normalized force in swing phase was extremely small for both species.

Table 12: Chimpanzee and human Total Normalized Muscle Force for each of the six static phase instances of the right arm climbing cycle. Normalized muscle force was an average of all 20 (chimpanzee) or 19 (human) muscle forces, and represents the average force for each muscle element in a given climbing phase instances.

	Normalized Muscle Force (%)	
Phase Instance	Chimp	Human
Early Support	7.435	26.814
Left Swing	8.815	16.924
Late Support	3.159	4.265
Early Swing	1.027	0.534
Mid Swing	1.970	1.369
Late Swing	1.371	2.225

5.6.4 Predicted Subacromial Space Width

Chimpanzees had a considerably wider subacromial space than humans in all six phasic instances of the climbing cycle (Figure 52). Differences between the two species were approximately 2 mm. The chimpanzee subacromial space varied between 11.3 and 14.1mm, whereas the human subacromial space was between 9.3 and 9.76 (Figure 52). The chimpanzee subacromial space was narrowest in late support when the arm was the most elevated.

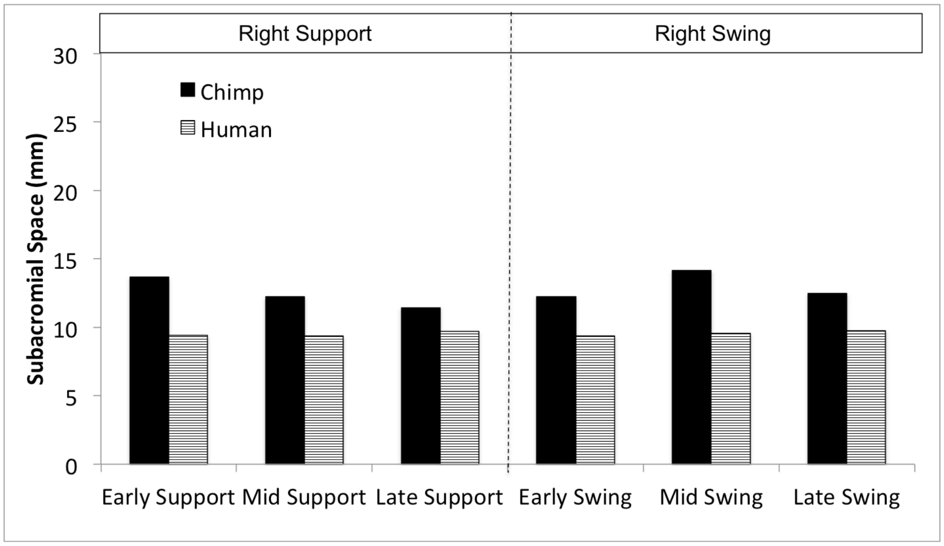


Figure 52: Predicted chimpanzee and human subacromial space during a single right arm climb cycle.

5.7 Discussion

This study developed a novel chimpanzee glenohumeral joint model for use in comparative musculoskeletal analyses. Comparisons with a parallel human glenohumeral joint model contrasted muscular and geometric differences between the humans and chimpanzees. These differences indicate musculoskeletal divergence that may associate functional differences with the evolutionary foundation of modern human function and rotator cuff pathology.

Both hypotheses were mostly confirmed in the present study.

Hypothesis one was supported, as the human glenohumeral model predicted higher muscle forces as a percentage of maximum force producing capability for most muscles, which mostly supported the second hypothesis. This hypothesis did not hold true for some muscles of the rotator cuff, triceps brachii and brachialis. However the total normalized muscle force was much larger for the humans than chimpanzees in support phase.

Hypothesis two was also supported by the model results. Chimpanzees were shown to have a wider subacromial space at all static instances of the climbing. The subacromial space was widest when the arm was lowered during swing phase, and when the arm reached forward into early support.

5.7.1 Model Evaluation

Evaluation of the novel chimpanzee glenohumeral model through concordance analysis provided evidence of the usefulness of the model. The results of the heuristic concordance analysis demonstrated a strong agreement between the timing of chimpanzee model predictions of muscle activity and experimental electromyographical measures of muscle activity for the same horizontal bimanual arm-suspension climbing task. With high agreement between measured and predicted muscle activity, the model can be considered sufficiently biologically realistic (Dickerson, 2005). This step provided the necessary evidence to allow comparative analyses to be conducted using the chimpanzee model with confidence.

The concordance analysis did not have complete agreement between model predicted and measured muscle activity timing, but the concordance value obtained was high. EMG is a very sensitive measurement technique. EMG results are dependent on muscle length, velocity of shortening, fatigue, muscle crosstalk, electrode placement, anatomical differences and processing techniques (Basmanjian & DeLuca, 1985; DeLuca, 1997). For this reason the present concordance analysis concentrated on muscle activity timing, as a concordance analyses that include muscle amplitudes would be susceptible to EMG variability and Type II error (DeLuca, 1997; Miller, 2006). A concordance value of 0.708 is considered satisfactory for an analysis of biological modeling (Dickerson, 2005). A few muscles had lower concordance, including subscapularis and posterior deltoid. This is not uncommon in optimization models using minimization cost functions. Realism in biological modeling is difficult as is requires the consideration of a variety of biological variables dependent on numerous parameters (Dickerson, 2005; Garner & Pandy, 1999). Model development requires compromise between biological realism and computational feasibility that can necessarily limit the overall results of model evaluation.

The evaluation of the chimpanzee glenohumeral model through a muscle force timing concordance analysis, while narrow, addressed the main output of the glenohumeral model. Numerous musculoskeletal outputs are possible from the model beyond muscle forces, including joint reaction forces, bone-on-bone forces, and dynamic stability ratios. However, the central output of the glenohumeral model was muscle forces due to their importance to joint function. Along with motion, the vast majority of glenohumeral stability is provided through active agonistic-antagonistic muscle pairings that compress the humeral head into the glenoid and direct the net joint reaction force into the glenoid (Veeger & van der Helm, 2007). Focusing the evaluation of the model on muscle force predictions was reflective of the core utility of the model.

Compromises and assumptions are required to develop efficient, purposeful models. The chimpanzee glenohumeral model developed in the present study was and is intended for comparison with parallel human and evolutionary models. The model's ability to distinguish different musculoskeletal strategies – particularly muscle force sharing strategies – from other models is its primary objective. Though imperfect, the present cost function was chosen as it improves agonist co-activation and muscle load sharing (Hughes, 1991). Assumptions and limitations present in the chimpanzee glenohumeral model are structurally mirrored in the comparator model(s). Of the three modules that comprise both glenohumeral models, the external torque and force prediction modules remained mathematically and structurally similar between the chimpanzee and human, with only a few anthropometric and postural differences. The geometric module was systematically changed at every step in developing the chimpanzee model, and represents the greatest computational difference between species. Therefore, differences between models are mostly representative of biological differences in the modeled musculoskeletal systems of the geometric module, and less so of the limitations to mathematical representations of biological phenomena. The lack of complete biological realism – including some synergistic and antagonistic muscle action – fall within the range of similar biomechanical models (Cholewicki et al., 1996;

Dickerson, 2005). The results of the present evaluation demonstrate that the chimpanzee model has value as a comparative model, providing insight into shoulder function and evolution.

5.7.2 Between Species Joint Kinetics Predictions

Large forces were experienced at the right glenohumeral joint during support phase of the climbing cycle in both the human and chimpanzee models. Large forces were expected, as supporting all or half of the body mass is required during support phase. The greatest forces are experienced during mid support/left swing, when the right arm is the only support arm. This requires the right upper extremity to support the whole body mass, doubling the already large hand force (Bergmann et al., 2011; Fleagle, 1977; Jenkins et al., 1978). The overhead reaching postures required to complete the climbing task also increased the joint forces. Elevated and abducted arm postures, as those observed in overhead reaches and climbing, further increase the joint reaction forces at the shoulder (Anton et al., 2001; Apreleva et al., 2000).

Changes to the joint reaction torques mirrored changes to joint position and orientation through support phase. Early support resulted in the largest torques in both the chimpanzee and human glenohumeral models. The support phase of the climb cycle can be viewed as the body mass moving under the right support hand like a simple pendulum (Chang et al., 2000). In early support, the position of the arm is akin to an anterior reach, and prepares the body mass to be accelerated by gravity as a pendulum at peak height (Figure 53) (Chang et al., 2000; Larson & Stern, 1986; Preuschoft & Demes, 1984). This phase created a large multi-directional torque, and required large muscle force recruitment to counter (Chang et al., 2000; Haslegrave et al., 1997; Sood et al., 2007). In mid support/left swing, while the applied hand force is greater, the body mass swings closer to the applied force at the hand, reducing the torque about all axes except joint flexion/extension, the local z-axis (Bertram et al., 2000; Preuschoft & Demes, 1984). By late support the body mass swings even closer to the applied force at the hand, to the pendulum's lowest height

(Figure 53), as double support is regained just prior to swing phase (Preuschoft & Demes, 1984). The applied hand force is half the previous phase, lessening the flexion torque and muscle action required to maintain an arm position near vertical, the direction of gravitation pull (Haslegrave et al., 1997; Larson & Stern, 1986).

Swing phase was marked by much lower joint reaction forces and torques. The external force was reduced to the mass of the upper extremity segments during swing phase, which require much lower muscle force to counter (Larson & Stern, 1986). The beginning of swing is marked by the hand releasing from the support rung in an elevated and highly externally rotated position (Larson & Stern, 1986). In early swing, elevation reduces, the arm abducts and external rotation lessens (Fleagle, 1977). By mid swing, the arm begins the anterior reach, and elevates against the pull of gravity (Larson & Stern, 1986).

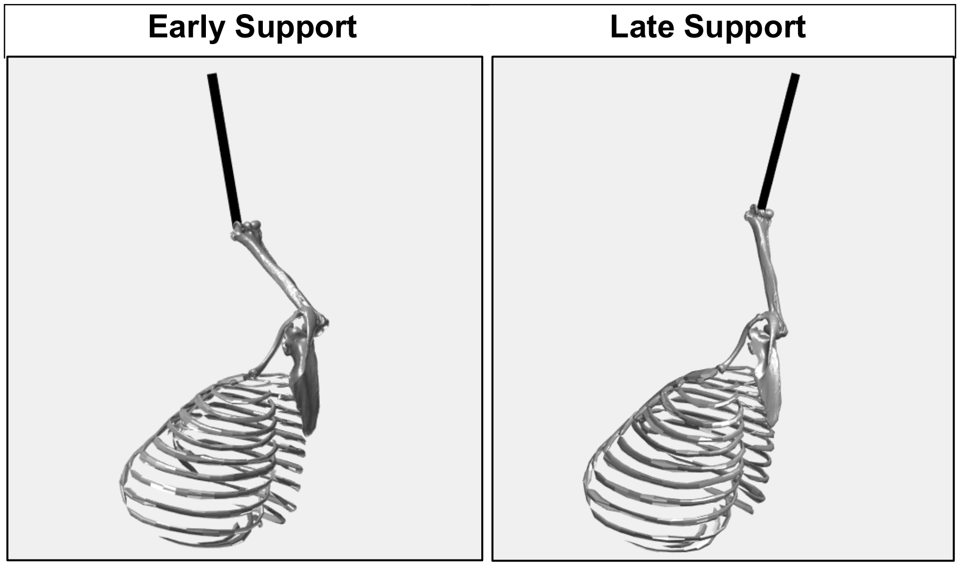


Figure 53: Arm position in early support and late support of the climb cycle. The arm is more elevated in late support than early support, and centered over the body mass.

5.7.3 Between Species Muscle Force Predictions

Chimpanzees executed the climbing task using an overall lower percentage of their muscular capacity than humans at all static stages of the climb cycle, at both the elbow and glenohumeral joint. This was expected, as chimpanzees have a greater muscle mass in their upper extremity (Walker, 2009). Humans have approximately 9% and 38% of their total body mass relegated to their upper extremity and lower extremity, respectively. Chimpanzees have 16% and 24% of their body mass concentrated in their upper and lower extremity, respectively (Zihlman, 1992). This difference in extremity mass proportions naturally translates into differences in upper extremity muscle mass. The average human can have a body mass that is 25kg greater than the average chimpanzee of 45kg (Carlson et al., 2006; Walker, 2009). However, chimpanzee upper extremity muscle masses can be upward of twice that of analogous human muscles, despite humans having a greater overall body mass (Mathewson et al., 2014; Thorpe et al., 1999). This translates into individual chimpanzee upper extremity muscles requiring a smaller percentage of their maximal muscle exertion to execute a task with the same posture and applied external force as humans.

Across all muscles in the present model, chimpanzees had a greater absolute physiological cross sectional area (PCSA). Even when scaled to the same body mass, chimpanzees still have greater relative PCSA across all muscles (Table 11) (Thorpe et al., 1999). There are notable muscles with a PCSA that was much greater than the human PCSA. These included coracobrachialis, middle deltoid, subscapularis, and supraspinatus. PCSA is directly related to force producing capabilities. Increased cross-sectional area increases the force production capabilities of a muscle by increasing muscle fiber content (Nigg & Herzog, 2007). That shoulder muscles in chimpanzees have a PCSA greater than humans demonstrates a large difference in force production capabilities between humans and chimpanzees (Thorpe et al., 1999). The most pronounced differences in PCSA may indicate the heightened importance of subscapularis, supraspinatus, and middle deltoid in producing rotational and stabilizing forces about the shoulder and glenohumeral joint in particular.

At the rotator cuff, muscular contribution from subscapularis and supraspinatus was almost exclusively only predicted in the chimpanzee glenohumeral model. While chimpanzees generally have a greater overall muscle mass and relative PCSA in their upper extremity than humans, the difference between species in each individual muscle varies. The entire rotator cuff, and each of its muscles are smaller in humans than chimpanzees (Larson, 2015; Sonneband & Young, 2009). However, the size of the four rotator cuff muscles with respect to each other also differs between species. Due to a wide breadth of upper extremity-inclusive locomotor behaviors, primates typically have a "subscapularis dominant" rotator cuff, unlike most other "infraspinatus dominant" mammals (Mathewson et al., 2014). Humans follow this "subscapularis dominant" pattern (Sonneband & Young, 2009). Yet the human supraspinatus and subscapularis are relatively smaller than other primates that habitually use their upper extremity in a climbing capacity (Inman et al., 1944; Larson, 2015; Mathewson et al., 2014; Sonneband & Young, 2009). That the chimpanzee rotator cuff includes a supraspinatus and subscapularis with greater absolute and relative PCSA indicates a greater capacity for producing forces to stabilize the glenohumeral joint (Larson & Stern Jr, 1986). The smaller size of the human supraspinatus and subscapularis may have made them less idealized for the strenuous task of climbing.

Activation of the deltoids differed between species as well, in both amplitude and timing. The deltoids are highly active during support phase, to raise the arm and counter traction at the glenohumeral joint from hanging and suspension (Larson & Stern Jr, 1986). Humans were predicted to activate all three deltoids to a much higher degree than chimpanzees. Chimpanzees have greater force producing capacity in their upper extremity muscles than humans, including the deltoids (Thorpe et al., 1999; Walker, 2009). Chimpanzees also have, on average, a lower body mass. As such, a lower percentage of their musculature is needed to complete the same postural task as humans. It was necessary for humans to recruit the deltoids relatively more as humans have a greater body mass to support, and the human deltoid muscles all had a lower absolute PCSA and subsequent force producing capability (Thorpe et al., 1999). The greater activation of all three deltoids in humans could have repercussions on shoulder function, as activation of arm abductors significantly decreases the subacromial space (Graichen et al., 2001).

The chimpanzee model predicted no contribution from the anterior deltoid in support phase, whereas the human model predicted the greatest contribution from the anterior deltoid. This may be due to differences in necessary muscle force production and muscle lines of action, as computational models are often very sensitive to variation in muscle lines of action (Nussbaum et al., 1996). The three heads of the deltoids have a broad base of origins on the scapula and clavicle, and contribute a superior force vector about the glenohumeral joint (Hart et al., 1985; Inman, 1944). The chimpanzee model required less individual muscle forces at each static instance of the climb cycle. Combined with muscle redundancy at the shoulder, the optimization routine was selective about which muscles are active in specific postures (Latash, 2012), targeting the most efficient prime movers. As the arm moved from an anterior, elevated position to a more posterior, elevated position, the deltoid partition that was best positioned to adequately activate in synergy with other glenohumeral muscles changed to achieve joint moment equilibrium.

Less multi-muscle contribution predictions in the rotator cuff could be problematic to the sustainability of weight-bearing climbing in humans. As habitual climbers, the chimpanzee glenohumeral joint routinely encounters greater forces than the human glenohumeral joint. Chimpanzees meet this demand with enlarged deltoids, subscapularis and infraspinatus. Both subscapularis and infraspinatus exert an inferior pull about the glenohumeral joint, countering the superior action of the deltoids and supraspinatus (Inman, 1944; Roberts, 1974). The entire modern human rotator cuff is smaller than the chimpanzees, with the subscapularis in particular being greatly reduced (Mathewson et al., 2014). This represents a necessary reduction in shoulder musculature to reduce segment masses and more efficiently redirect muscular effort toward modern needs such as carrying, tool manipulation, throwing and communication (Wood & Richmond, 2001). However, with less action from the weaker subscapularis to counter the superior action of the deltoids, the infraspinatus becomes the primary preventative means to superior migration of the humeral head and reduction of the subacromial space. The human model predicted high muscle forces from the infraspinatus and teres minor to provide inferior forces about the glenohumeral joint. As the teres minor is a very small muscle in humans that contributes minimally to the inferior force vector about the glenohumeral joint, this creates a likely scenario for infraspinatus fatigue. Along with superior humeral head migration, fatigue of the infraspinatus can reduce posterior tilt and lateral rotation of the scapula necessary to widen the subacromial space in overhead postures (Borstad et al., 2009; Ebaugh et al., 2006; Tsai et al., 2003). As chimpanzees have large infraspinatus and subscapularis to counter the deltoid, this may guard against overload of a single muscle.

5.7.4 Between Species Glenohumeral Geometry

The subacromial space was wider at all static instances of the climbing cycle in the chimpanzee model, a possible geometric mechanism for reduced subacromial impingement risk in the species. The difference between species was approximately 2mm throughout the entire climb cycle. Reports on the width of the human subacromial space have varied widely between 2-17mm, due to differences in arm posture, measurement techniques and anthropometrics, particularly the shape of the acromion (Bey et al., 2007; Petersson & Redlund-Johnell, 1984). The average human subacromial space is usually about 8-10mm (Petersson & Redlund-Johnell, 1984). The laterally projecting human acromion is typically sloped inferiorly, unlike chimpanzees, which can reduce the width of the subacromional space (Voisin et al., 2014). As the arm is elevated, the subacromial space decreases in humans (Bey et al., 2007; Graichen et al., 2001). The results of the present study seem to indirectly demonstrate a similar trend in chimpanzees, as the subacromial space was lowest in late support. However, the chimpanzee subacromial space still remained greater than the average widths seen in humans, close to 12mm. The increased space between the humerus and acromion in chimpanzees would provide a greater berth for tendons in the subacromial space, like supraspinatus, throughout the range of shoulder elevation, reducing the risk for impingement of tissues (Lewis et al., 2001). While the reduction in size and absolute PCSA of the supraspinatus in humans brought about decreases in force production, it is likely associated to accommodation of a narrower subacromial space (Voisin et al., 2014).

As they habitually climb as a form of locomotion, chimpanzees have superiorly oriented glenoid, scapular spine and acromion, which differ from the modern human lateral glenoid, scapular spine and acromion orientation. The chimpanzee superior orientation optimizes the entire glenohumeral and acromioclavicular region for overhead behaviors and tasks (Larson, 2007). The superiorly orientated chimpanzee scapular spine and glenoid, much like other climbing primates, reorients the lines of action of the deltoids, and rotator cuff to optimize overhead behaviors, particularly propulsive arm swinging motions (Larson, 2007; Larson & Stern, 1986; Roach et al., 2013). Muscles like supraspinatus, infraspinatus and the subscapularis have increased moment arms in overhead postures in chimpanzees, as the lines of action become optimized from origin to insertion (Larson, 2015). The laterally oriented human glenoid establishes the human range of motion as ideal for the use of the hands in front of the body for tool manipulation and carrying while also optimizing the glenohumeral muscle lines of action for lateral motions such as throwing (Larson, 1988; Roach et al., 2013). Humans also have an enlarged and widened acromion process, and lateral projection of the acromion over the glenohumeral joint (Schultz, 1968; Voisin et al., 2014). The lateral projection of the acromion changes the mechanical leverage of the deltoids, shifting the muscle origin to be over the joint. This improves the deltoid moment arm in below-the-shoulder action and compensates for the reduced force production of the supraspinatus muscle (Lewis et al., 2001; Voisin et al., 2014). However, this projection also reduces the subacromial space, resulting in higher injury risk for impingement in humans (Larson, 2007; Lewis et al., 2001; Voisin et al., 2014). Many of the differences between humans and chimpanzees muscle activation patterns can be associated with the superior-inferior reorientation of the glenohumeral joint, scapular spine and projecting acromion.

The difference between species in glenohumeral stability also likely affected predicted muscle activity patterns. Humans and closely related primates have very similarly shaped glenoid fossae (Voisin et al., 2014). However, analysis of the human and chimpanzee glenoid indicate a deeper glenoid in chimpanzees. The deeper glenoid in chimpanzees increases intrinsic stability by increasing the ratio of compressive force needed for an applied shear force at the glenohumeral joint (Lugo et al., 2008), but at the cost of some postural flexibility. This reduces the demand on muscles to produce stabilizing forces to counter shearing forces about the glenohumeral joint (Matsen et al., 1994; Veeger & van der Helm, 2007). The greater depth of the chimpanzee glenoid provides another explanation for lower muscle forces in chimpanzees, as required active muscular contributions to stabilization would be lowered.

Along with glenohumeral orientation, the scapular body shape is hypothesized to affect behavior of the rotator cuff muscles. Chimpanzees have a longer, narrower scapula compared to humans, along with their more superiorly oriented glenoid and scapular spine. Changes to the shape of the scapular body affect the shape and size of the infraspinatus, supraspinatus and subscapularis fossae, and muscle lines of action as they cross the glenohumeral joint (Roberts, 1977). Distinct scapular body shapes have been inferred to represent changes in muscular action, including increased fossa size in arm-suspension climbing primates to increase muscle size to compensate for lower joint stability (Larson, 2015; Larson & Stern, 2013; Potau et al., 2009). This inference was supported in a study that enforced a change in locomotion on rats that demonstrated significant alterations in the shape of the scapula. Rats that were constrained to bipedal locomotion instead of their normal quadrupedal locomotion developed scapulae that were more similar to humans, including shorter and wider body shape, a more dorsal position and rotation, and a change in the surface area of the infraspinatus fossa (Riesenfeld, 1966). However, a more recent study on scapular body morphology and rotator cuff function between three primate species of different locomotor habits found no correlation between scapular fossa size and rotator cuff function between species (Larson & Stern, 2013). Fossa size alone is unlikely to affect joint function, without concurrently affecting mechanical function of the muscle through changes to origins and insertions, lines of action, and moment arms about the joint(s) they influence (Ward et al., 2006). Differences between chimpanzee and human scapular body shape may have contributed to the different actions of the rotator cuff in the present study, but likely by altering the line of action of the rotator cuff muscles as they crossed glenohumeral joint.

5.7.5 Effect of Musculoskeletal Differences on Modern Human Function

While musculoskeletal form relates to functional adaptations, by how much is uncertain. The gross structure of the upper extremity is common in all mammals, with adaptations specific to the behaviors and locomotion of each species (Martin-Serra et al., 2014). The skeletal composition of the chimpanzee and human shoulder region is very similar (Crompton et al., 2008; Young et al., 2015). However, geometric morphometric comparisons between the two species – particularly of the scapula – have yielded varying and puzzling results regarding the importance of physical features of the bone to function (Churchill et al., 2013; Haile-Selassie et al., 2010; Green & Alemseged, 2012; Oxnard, 1967, 1977). Changes in bone shape due to changes in necessary muscle forces are generally minimal in closely related species, and not always associated with resultant changes in soft tissue (Larson, 2015). However, small changes in bone shape and orientation can greatly affect muscle lines of action and moment arms (Ward et a., 2006). Differences in muscle mechanical arms are often the most notable biomechanical differences between similar species that mark differences in muscle force producing capacity and efficiency (Biewener, 1990). The relationship between form and function, particularly for muscle function, is likely strongest when considering how changes in bone morphology alter muscle mechanics about a joint.

The reduced absolute and relative PCSA, altered scapular shape, and composition of the rotator cuff and deltoids may be evolutionary indications of why humans have a propensity for subacromial impingement syndrome that does not exist in other primates. The particular structure of the primate rotator cuff is hypothesized to be for overhead postures and locomotion (Larson, 2015; Sonneband & Young, 2009;

Roberts, 1974). Humans share this gross rotator cuff structure with primates, but are much more susceptible to subacromial impingement and rotator cuff tears compared to other primates (Lewis et al., 2001). The rotator cuff and deltoids form a series of force couples around the glenohumeral joint that act to center the humeral head in the glenoid (Larson & Stern Jr, 1986). The superior unit of the force couples is comprised of the deltoids and supraspinatus, which elevate the arm, while the inferior unit is comprised of the rest of the rotator cuff, which depress the arm (Inman, 1944). Humans have a supraspinatus and middle deltoid with much lower force production capabilities. This has reduced the ability of the human shoulder to elevate the arm (Larson & Stern Jr, 1986). Infraspinatus and subscapularis are the strongest and thus most important resistors of superior migration of the humeral head in humans caused by the deltoids (Chopp et al., 2010). That lower force producing capability of subscapularis in humans represents an evolutionary adaptation that has also reduced its contribution to centering the humeral head in the glenoid (Potau et al., 2009). This has increased the susceptibility of humeral head to superior migration and subsequent subacromial space impingement. Deleterious consequences of superior migration of the humeral head are compounded in humans, due to the more lateral projection of the acromion over humeral head and the less superior orientation of the acromion (Larson, 2007; Voisin et al., 2014). Chimpanzee maintenance of a superiorly oriented glenohumeral joint, less projected and more superiorly oriented acromion, and rotator cuff with greater force producing capacity may explain why primates experience fewer subacromial injuries despite a preponderance of overhead postures.

The modern human rotator cuff has evolved for below shoulder, low force behaviors. The rotator cuff has a relatively low PCSA and force producing capability and crosses a laterally orientated joint (Larson, 1986; Thorp et al., 1999). The modeled bimanual climbing task does not represent a modern task the human upper extremity has evolved to perform. Rather, low force, non-locomotor tasks such as reaching, pushes and pulls, carrying, and tool creation and manipulation are more modern representatives of human behavior (Woods & Richmond, 2001). Axial rotation and stabilization of the arm are provided by co-activity of the rotator cuff, typically below shoulder height (Lee et al., 2000; McKernan et al., 1990). Though not optimized for recruitment in bimanual climbing, muscles such as supraspinatus and subscapularis are highly selected for lower elevation, lower force, push tasks and arm internal rotation tasks (Lee et al., 2000; McDonald et al., 2012). In these modern tasks, more dispersed rotator cuff activity across all four muscles is observed.

The evolved potential for fatigue-related injury from bimanual climbing is a reflection of the injury risk detected in other more modern, common and low-force overhead behaviors. Overhead and repetitive tasks are strong predictors of shoulder pain and eventual development of disorders (Andersen et al., 2003; Hughes et al., 1997; LeClerc et al., 2004). Arm elevation is associated with an increase in muscle activity at the shoulder (Anton et al., 2001). In particular, the activity of the deltoids increases with increasing arm elevation (Anton et al., 2001; Sood et al., 2007). This is problematic, as deltoid activity must be matched by an increased activation from the rotator cuff muscles. The rotator cuff has a primary role in the abduction and axial rotation of the arm, as well as stabilization of the humeral head into the glenoid, countering the superior pull of the deltoids (Yanagawa et al., 2008). However, in increasingly elevated, overhead postures, the rotator cuff counter-pull is compromised due to the evolved reduction of mass and PCSA in the rotator cuff relative to the deltoids. The rotator cuff must be recruited at a greater percentage of maximum to stabilize the glenohumeral joint, even in low force tasks. Many occupational settings require overhead postures for job completion. That these tasks are often necessarily repetitive leads to muscular fatigue (Ebaugh et al., 2006; Nussbaum et al., 2001), and eventually shoulder pain and pathology (Andersen et al., 2003; van der Windt et al., 2000). The present bimanual climbing task represents a more extreme version of overhead behaviors. The model predicted over-exertion of infraspinatus and teres minor, which would rapidly initiate fatigue and injury. In modern work places this injury mechanism occurs through the same pathway, but with less expedience. This relates the modern propensity for work-place injury to the evolution of the shoulder away from overhead postures and high force tasks.

5.7.6 Limitations

There were a series of assumptions and limitations to the development of the chimpanzee glenohumeral model and the computational comparison between humans and chimpanzees. Computational musculoskeletal modeling offers numerous benefits to biomechanical study of the human body. However, several limitations constrain the present modeling of the glenohumeral joint. Though not documented in the current study, there are potentially important differences between humans and chimpanzees in the hand and forearm musculoskeletal composition that could contribute to differences between species in climbing technique and ability (Stern & Larson, 2001; Thorpe et al., 1999). The shoulder is considered a three-joint structure, and the acromioclavicular and sternothoracic joints were not considered, though the torso and clavicle were geometrically positioned to dictate the position of the scapula and influence shoulder rhythm (Voisin, 2006). Chimpanzees also have different upper extremity muscle architecture than humans (Carlson, 2006; Thorpe et al., 1999; Walker, 2009). Beyond physiological cross-sectional area, this was not accounted for in the present model. Though chimpanzees have more of their body mass and muscle mass concentrated in their upper extremity than humans, this does not completely explain differences in force producing capabilities between the two species. While total mass does increase the maximal force of a given muscle, muscle architectural properties also influence muscle function (Powell et al., 1984; Winters et al., 2011). Ligaments were set as inactive in both models, and did not contribute to joint stability. As glenohumeral ligaments are known to be most active at end-range of motion, this may not have reflected biological reality. However data is not available on chimpanzee shoulder ligament behavior. As well, the models were designed to be muscle-driven, with a focus on synergist muscle predictions. Combined with lack of ligamentous data, it was considered appropriate to remove the effect of ligament support from both models. Additionally, optimization routines, as used in the glenohumeral model, can often overlook the contribution of small muscles to a task in favor of larger muscles with greater force producing capabilities (Dickerson et al., 2007). Computation musculoskeletal modeling is limited by how researchers can mathematically represent biological phenomena. To model the entirety of the human musculoskeletal system is computationally expensive and often leads to more assumptions, difficulty in interpretation, and erroneous results (Cholewicki et al., 1995). Assumptions are crucial in producing models that adequately address the primary research questions at hand. The present model set out to compare the glenohumeral musculoskeletal behaviors between two species, particularly differences in muscle patterns. The models are considered to have achieved this purpose.

The postural analysis run in the present study did not replicate the full breadth of differences between chimpanzees and humans. The kinematic inputs for both models were derived from human experimentation. While the human data was modified to represent the geometry of the chimpanzee shoulder for the chimpanzee model, the kinematics may not exactly mimic those a chimpanzee would use. However, if the kinematic inputs are not representative of a chimpanzee climbing kinematics, then the results of this comparison between species are likely more conservative than one that uses kinematics that varied more between the two models. The model was run statically, not dynamically. This negated the effect of motion and momentum, which would influence joint forces, and muscular recruitment patterns in a powerful and propulsive behavior such as brachiation (Larson & Stern, 1986). Assumptions were made about hand force in each of the support phase static instances. Hand forces will change gradually over a climb cycle depending on whole body and upper extremity postures, anthropometrics and climbing pace, and would rarely be explicitly only whole or half body mass. For the initial static analysis, whole or half body mass operated as a provisional representative of hand force in the three support phase static instances of the climb cycle. Future experimental analyses that include hand force recordings would provide greater insight into application of appropriate hand force for both static and dynamic bimanual climbing task analyses. A static analysis was considered the most appropriate initial analysis to make comparisons between species in glenohumeral function due to the complications of assumptions required for dynamic modeling of the climb cycle. The models are both capable of running dynamic assessments of climbing for future study.

The models are both limited by the choice of individual and musculoskeletal data used to represent each species. Each model was run using postural inputs from a single individual. As well, the geometry module of both models used bone scan inputs from a single, different individual. Other musculoskeletal features and parameters, such as segment parameters, muscle PCSA, origins and insertions, relied on collected and dissected data from a variety of published databases. As large variability exists in both kinematics and bone geometry of both species, each model in limited by how much the motion data and musculoskeletal geometry represents an average individual. The human data from databases often represent older populations, which can greatly affect PCSA values. For this reason, human absolute PCSA values were doubled (Dickerson, 2005). The human postural data was selected as the participant represented an average male with kinematic data that fell near the mean values described in Study 1, Chapter 3. However, the modifications made to this data to be chimpanzee-like, may not represent average chimpanzee kinematics. The best approximation of this was made in the two-dimensional qualitative comparative analysis in Study 1. Without further chimpanzee video or kinematic data, it is difficult to interpret the likelihood of the kinematics being representative of average chimpanzee motion data. Much of the chimpanzee musculoskeletal data was taken from chimpanzees in captivity. Primates in captivity typically behave differently than wild primates, often brachiating less (Stevens & Carlson, 2008). This can result in the development of different skeletal geometry, muscle mass and PCSA, and kinematic strategies (Sarmiento, 1985). There is limited data on chimpanzees however, so the data utilized in the present study represented the best options to develop the chimpanzee model. Should improved musculoskeletal or motion data become available, the model would be highly receptive of new modular parameters.

Unique assumptions related to chimpanzee musculoskeletal behavior were incorporated into the creation of the chimpanzee model, owing to limited data on chimpanzees. The shoulder rhythm algorithms were adapted from a previously developed human shoulder rhythm and used two-dimensional x-rays to define modified chimpanzee scapular and clavicular orientations. Scapulothoracic contact force application sites, joint centers, and glenohumeral contact force constraints were estimated from regression equations designed for the human upper extremity. Specific tension was assumed to be equivalent to human estimates. While the optimization objective function has been applied repeatedly to evaluate human shoulder function, the chimpanzee shoulder is used for many weight-bearing tasks for which the human shoulder is not (Bertram et al., 1999). This could alter the muscular activation and load sharing in the chimpanzee shoulder. Model evaluation was limited by the small amount of quantitative data available on chimpanzee upper extremity geometry, kinetics and muscle activity. The paucity of complete information required considerable flexibility, experimentation and adaptability during the construction of this model. However, the model was created to enable efficient algorithm adjustment based on alternative hypotheses, and to allow modifications as novel future musculoskeletal and kinematic data on chimpanzees exists. The very existence of the initial exploratory model is imperative for progress and success of future studies on primate evolutionary shoulder function.

Finally, the computational comparison between species is limited in its generalizability, due to the limitations of the primate species selected. Chimpanzees represent one, extant primate shoulder, closely related to modern humans. Other living primates, such as orangutans, gorillas, and gibbons are also closely related to humans. These species have unique similarities and differences from humans, and chimpanzees, which would also prove useful in understanding function of the human shoulder (Schmidt & Kraus, 2011; Young, 2005, 2008). The chimpanzee was selected for its functional and musculoskeletal structural similarities to humans, as well as availability of comprehensive data. Future analyses could consider other interspecies comparisons. Analyses with more primate species of varying upper extremity usage and specialties would better parse out the specific features of the human shoulder that dictate its function. Extinct hominin species could also be used as comparator models, however data is limited on these species, particularly muscular properties. Such comparisons would require many more assumptions than those in the present study.

5.7.7 Future Directions

The chimpanzee model was developed as highly amenable to adaptations and alterations. As the model includes four segments – torso, humerus, clavicle, and scapula – it is possible to include improved representations of chimpanzee acromioclavicular and sternoclavicular joints to broaden the musculoskeletal outputs to include the entire shoulder complex, and add new chimpanzee musculoskeletal data as it becomes available. The model also calculates dynamic outputs, which were not explored. Finally, additional model outputs are possible, beyond those in the present study. Such outputs, including stability ratios and bone-on-bone joint forces, can be incorporated into future comparative analyses. These avenues are worth exploring in future to expand on the current results.

Only one, evolutionarily relevant task was considered in the present study. Further analyses of other functional and evolutionarily relevant tasks, such as vertical climbing, throwing, simple tool manipulation, and reaching, would corroborate and strengthen the present conclusions regarding shoulder geometry and muscle function in primates and humans.

5.8 Conclusion

While prevalent in biomechanics and engineering, computational modeling is still very new and unexplored in evolutionary science. Classical measuring techniques in physical anthropology have deep-rooted limitations that often discount the manner in which features of the musculoskeletal form operate synergistically as a system

(Hutchinson, 2012). Computational models such as the presently developed chimpanzee model allow assessment of specific features of the musculoskeletal system, and how they interact to produce movement at the shoulder. Model parameters can be adjusted and altered to address alternate scientific questions, including changing bone shapes, bone and orientations, and muscle architecture and insertions and origins.

Beyond benefitting evolutionary science and curiosity, primate computational models also provide benefits to exploring and answering modern human concerns. Humans often reach critical physical limitations, and there are still many unanswered questions regarding human capacity and risk for joint injury and disorders. Computational models provide a controlled simulation environment to explore the human shoulder musculoskeletal system as it compares to closely related species with vastly different behaviors. These models become particularly salient when used to simulate tasks that have highly different efficiency between species, such as climbing in humans and chimpanzees. Differences in function can be quantified in the context of measurable differences in musculoskeletal geometry. When these evolutionary differences are applied to modern human function, a better understanding of how the shoulder operates is achieved. Understanding evolutionary adaptations that have brought about the modern human shoulder can aid our understanding of specific strengths and weaknesses of the modern shoulder, root causes of injury risk, and how to avoid them.

The present results confirm that while chimpanzees and humans have very similar gross musculoskeletal anatomy, changes to glenohumeral skeletal geometry and muscle PCSA influence joint kinetics and muscle force production in overhead postures. These changes corroborate shoulder injury and disorder rates in humans. The superiorly orientated glenoid has opened up the chimpanzee glenohumeral joint for overhead behaviors. The associated superior angle of the acromion that is also less projected over the humeral head in chimpanzees widens the subacromial space, reducing the risk of impingement. Humans have reduced sizes and absolute PCSAs of many of the muscles crossing the glenohumeral joint to accommodate modern, below-the-shoulder, non-weight-bearing upper extremity behaviors. However, this reduction in PCSA is not uniform, as some muscles have relatively lower force capacity than others. This has modified the force couples that act to stabilize the humeral head in the glenoid fossa. As a result, muscles like infraspinatus may become overloaded and highly susceptible to fatigue when countering the superior pull of the deltoids. When infraspinatus becomes fatigued, the humeral head migrates, narrowing the already narrower human subacromial space. While these adaptations have enabled essential behaviors like tool manipulation, throwing and carrying, they may also explain the modern human propensity for subacromial impingement and rotator cuff tears.

Chapter 6 Study 4: Development of a Probabilistic Chimpanzee Musculoskeletal Glenohumeral Model

6.1 Introduction

Morphological comparisons are common in physical anthropology, and have led to major breakthroughs in functional adaptations to the musculoskeletal form. Much of present knowledge regarding human evolution arose from comparative morphology (Pontzer et al., 2009). Morphological comparisons are often built upon morphometrics – a statistical method of analyzing the relationship of specific morphological features that are related to each other and comparing morphology between taxa (Larson & Stern, 2013, Young et al., 2015). Comparing and contrasting boney features between primate species and fossils enables meaningful associations of the physical capabilities and locomotor behaviors with modern function. However, this method has the potential to produce equivocal results. It is also problematic to determine which features are most important and most related to each other (Young, 2003). Certain features vary markedly even within species, and the influence of this plasticity on functional ability is unknown (Collard & Wood, 2000). Comparative morphological analyses serve to correlate morphological features, and contrast species; but they are unable to fully assess how these features contribute to the distinction of each species. To refine the delineation of morphological contributions to physical behavior, computer models are critical (Hutchinson, 2012).

Comparing fossils and extant species can contribute to the understanding of evolutionary adaptation. Not all morphological evolutionary adaptations have a positive adaptive value (Cartmill & Smith, 2009; Young et al., 2015). Some are consequential or side effects of a more adaptively valuable morphological change. Changes favored by natural selection can initiate undesirable concomitant changes. Thus, some evolved morphological traits observed in extinct and extant fossils may be trivial or disadvantageous. This makes the method of evaluating and analyzing morphology through an “itemized” comparative approach problematic (Lovejoy et al., 1999). Since the entire organism acts as a system, slight variations through development and growth are accumulated, and modify other parts of the system. To explain this phenomenon, comparative biomechanics needs to provide a rationale for associating or correlating specific adaptations with modified system physical function.

Central issues arise from traditional approaches to associating morphological form with musculoskeletal function. First, the chosen method of analysis can affect conclusions regarding the specific role of the musculoskeletal traits in locomotion. Various methods are used by anthropologist to measure the size and shape of desired musculoskeletal traits. Unfortunately, the choice of method used for measuring traits like attachment site size of muscles can alter the determined size and the accuracy of different methods may vary depending on the species and muscle being examined (Larson & Stern, 2013). Similarly, multifactorial analyses demonstrate different outcomes depending on the number and type of musculoskeletal variables considered in the model (Churchill et al., 2013; Green et al., 2016). The relationship between morphological form and physical ability and locomotion is dependent on the types of morphological features chosen, how many are chosen, and the statistical technique used (Churchill et al., 2013; Oxnard, 1969).

A second limitation of using traditional anthropological methods is that muscle function during locomotion is multifactorial and associated with numerous boney features; this further complicates the association between form and function. The locomotor behaviors of each primate, and frequency of each behavior, affect how the upper extremity is used and operated (Larson, 2015). Species-specific orientation in each of the bones required for locomotion can affect attachment site and size, muscle size and mechanical leverage of multiple muscles in the upper extremity (Larson, 1988; Larson & Stern, 2013). A change in the orientation of the elbow through humeral torsion can alter how much internal and external rotation of the arm is necessary to brachiate, which can alter activation of subscapularis, independent of attachment site size (Larson, 1988). An enlarged projection of the greater tubercle of the humerus could increase the moment arm of the infraspinatus muscle, improving mechanical leverage by requiring a relatively smaller muscle to produce a similar moment about a joint (Taylor, 1997). A small muscle footprint for a particular muscle may be less indicative of weaker muscle strength than increased reliance on another, more mechanically effective, agonist (Churchill & Rhodes, 2009). Defining how small changes in musculoskeletal form potentially affect musculoskeletal function requires a probabilistic modeling approach that integrates multiple musculoskeletal factors into simulating locomotor task completion.

Thus, individual or select morphological features should not be considered in isolation, but must be contextualized as part of a complex and plastic system. Identical bony morphology in two different species may potentially yield different behaviors due to changes in the musculoskeletal system. This may create different roles for similar physiological or morphological traits (Lauder, 1995). Computer models that can simulate small morphological changes give greater insight into how specific traits affect physical ability and joint function (Chopp-Hurley et al., 2016). This is especially true of the shoulder. The complexity of the shoulder, and scapular morphology in particular, makes conclusions regarding the development of species-specific characteristics difficult and infeasible using traditional morphological comparison methods (Young, 2003). Probabilistic musculoskeletal modeling can help to identify candidate traits that are integral to each species' physical ability. Such modeling may help to settle persistent debates regarding the evolutionary relationship between form and function in primates and humans.

Probabilistic computational modeling can give new insight into the manifestation of functional variability within human populations and between species. The modern human shoulder is susceptible to injury in overhead and weight-bearing postures (Lewis et al., 2001; Young et al., 2015). Computational models can incorporate known or suspected musculoskeletal differences in a variety of tasks, postures, and morphologies. This allows crucial simulation of injury mechanisms, as they are often multifactorial, and dependent on both kinematics and morphological variations (Chopp-Hurley et al., 2016). However, even deterministic models lack consideration of the breadth of variability of the determinants of injury within a population

(Langenderfer et al., 2006). Small iterative changes to the parameters within musculoskeletal models, much like in biological organisms, can result in important changes in musculoskeletal function (Chopp-Hurley et al., 2014; Hutchinson, 2012; Larson, 1998; Young et al., 2015). Probabilistic approaches to computational modeling not only build upon the geometric morphometric analysis conducted in evolutionary science, but also the deterministic musculoskeletal models in biomechanics. This approach provides new mechanisms for capturing the effect of physiological variation between individuals, populations and species. To fully understand the effect of evolutionarily relevant physical features on the distribution of modern human glenohumeral function, the full effect of species variation on those features must be explored through a probabilistic computational approach.

6.2 Purpose

The purpose of this study was to create a probabilistic musculoskeletal model of the chimpanzee and human glenohumeral joints to assess the contribution of different boney features to muscular effort of the rotator cuff in the performance of an evolutionarily significant upper extremity task. An overview conceptual framework is featured in Figure 54. The morphological features selected for probabilistic analysis were those deemed to have anthropological relevance to the great ape evolutionary divergence, and noted in Chapter 5 Study 3 as reflecting baseline differences between the chimpanzee and human deterministic model results. These features include:

- Rotator Cuff origins on the scapula
- Deltoid insertion on the humerus
- Glenoid superior-inferior orientation
- Glenoid depth as an indicator of glenoid stability

6.3 Hypothesis

It is hypothesized that differences will exist between species in rotator cuff muscle forces:

Hypothesis one – Alterations of superior-inferior glenoid inclination, and muscular lines of action of the infraspinatus, subscapularis and supraspinatus, will cause recruitment of all rotator cuff muscles in humans and greater convergence with predicted chimpanzee muscle forces, when previous deterministic analysis limited recruitment to infraspinatus and teres minor.

Hypothesis two – Perturbing the insertion of the deltoid on the humerus will change the contribution of the deltoids to stabilizing glenohumeral muscle forces, resulting in changes to the contribution from supraspinatus in both species.

Hypothesis three – Varying the stability ratios of the glenoid fossa will change the recruitment of rotator cuff muscles by altering the amount of muscular force necessary to compress the humeral head into the glenoid.

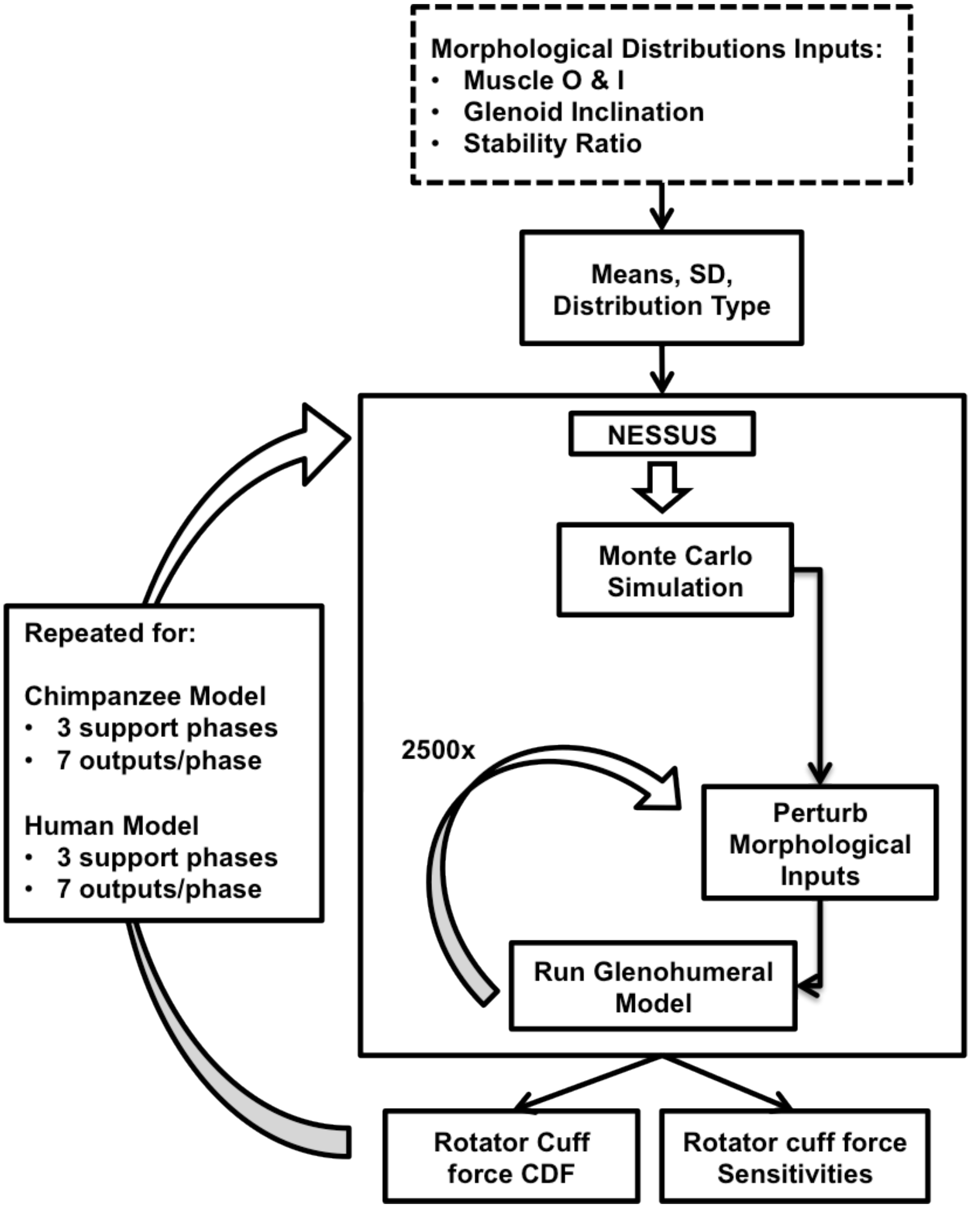


Figure 54: Flowchart of the creation and running of the Study 4 probabilistic chimpanzee and human models. Probabilistic inputs are in dashed boxes, and will be distributions of human chimpanzee morphological traits. Probabilistic outputs for both the human and chimpanzee models are at the bottom. O & I = origins and insertions. SD = standard deviation. CDF = cumulative distribution function.

6.4 Methods

The developed human and chimpanzee musculoskeletal models are intentionally designed to be geometrically scalable. This allows the geometric module of the models to be modified to emulate known variability in specific musculoskeletal features within each species. This scalability was used to create a probabilistic chimpanzee and human model by varying specific glenohumeral morphological traits. The probabilistic model was then used to quantify the effect of the morphological variability of these traits on rotator cuff muscular effort patterns.

6.4.1 Geometric Module Scaling and Probabilistic Variables

6.4.1.1 Probabilistic Inputs

Based on the deterministic results of both the chimpanzee and human glenohumeral models, and anthropological literature, specific geometric parameters were chosen as inputs to be perturbed in the probabilistic analyses. Features that are presumed to affect glenohumeral function were selected from primarily the scapula, as well as one from the humerus (Table 13).

Table 13: Morphological Features used as inputs to the probabilistic chimpanzee and human glenohumeral models. The specific computational variable perturbed in each model is also given, along with the anthropological significance for feature selection.

Input Feature	Perturbed Model Inputs	Rationale
Scapular origins of the rotator cuff muscles	Origin Coordinates: Infraspinatus origin [X,Y,Z] Subscapularis origin [X,Y,Z] Supraspinatus origin [X,Y,Z]	Mimic changes to scapular body shape. Associated with rotator cuff lines of action (Larson, 1998)
Deltoid insertion on the Deltoid Tuberosity	Insertion Coordinates: Anterior, Middle and Posterior Deltoid insertion [X,Y,Z]	Arm abductors associated with capacity for overhead postures (Larson, 1995)
Glenoid Inclination	Superior-Inferior Y-axis of Glenoid Coordinate System	Superior inclination may optimize joint for overhead behaviors (Larson, 1998)
Intrinsic Stability of the Glenoid	Multiply directional stability ratios by additive factor	Modifies muscle forces required for active joint stabilization (Veeger & van der Helm, 2007)

The three-dimensional coordinates of infraspinatus, supraspinatus, and subscapularis muscle origins and deltoid muscle insertion were already explicitly coded into both models and were used to perturb each of these muscle positions. Landmarks that define each of these characteristics are shown in Figures 55. All landmarks are three-dimensional [X,Y,Z] coordinates, locally expressed as a percentage of bone length, in the coordinate system of the specific bone. Each muscle origin or insertion was varied along all three dimensions. The scapular coordinate system x-component represents superior-inferior directional changes along the length of the scapular body, y-component represents medial-lateral directional changes along the width of the scapular body, and the z-component represents anterior-posterior directional changes to the muscle origins of infraspinatus, subscapularis, and supraspinatus. On the humerus, the coordinate system x-component represents superior-inferior directional changes along the length of the bone, the y-component represents the anterior-posterior directional changes, and the z-component represents the medial-lateral directional changes to the deltoid insertion. Infraspinatus and subscapularis have multiple muscle elements. To simplify the probabilistic simulation, the upper infraspinatus and upper subscapularis were directly probabilistically modeled. The other infraspinatus and subscapularis muscle element positions were dependent on the perturbed position of the upper element and were probabilistically modified through perturbation of the upper element. Each of the original three-dimensional coordinates of the middle and lower elements of these muscles were converted into percentage differences from the upper element's three-dimensional coordinates. This forced these muscles to act as a unit in the probabilistic model.

Glenoid inclination was varied by altering the y-axis vector of the local glenoid coordinate system. The y-axis vector of the glenoid coordinate system is comprised of the superior landmark of the glenoid (vector tip) and centroid of the glenoid (vector tail). To change the angle of the y-axis vector, the superior landmark of the vector – which identified the superior point of the glenoid in global three-dimensional [X,Y,Z] coordinates – was shifted in the mediolateral direction (Figure 56). This required perturbation of the global y-value of superior glenoid [X,Y,Z] coordinates only, which represents the global mediolateral dimension of the landmark. Shifting this single value varied the identification of the superior-inferior inclination of the glenoid in each model (Figure 56). The y-value of the glenoid superior landmark was already explicitly coded into the model as part of the identification of the glenoid coordinate system and orientation.

All eight directional glenoid stability ratios were altered to have an additive factor. In Chapter 4 Study 2, the chimpanzee glenoid was modeled as 1.205mm deeper than the human glenoid (Lippitt et al., 1993; Matsen et al., 1994), representing a 13.13% increase in each of the eight directional stability ratios. This additive factor of 13.13 was explicitly coded into the chimpanzee glenohumeral model. In the human glenohumeral model, a corresponding additive factor of mean = 0.00%, was applied to each of the eight stability ratios. This value, along with the previously applied additive factor of 13.13 in the chimpanzee model represented the baseline values that were perturbed to vary intrinsic stability of the glenoid.

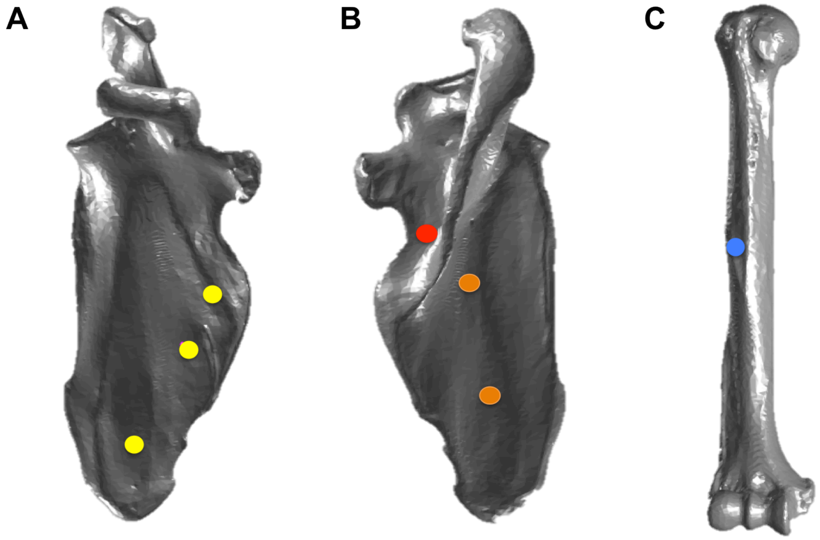


Figure 55: Original three-dimensional muscle landmark positions on the scapula and humerus representing the (A) subscapularis (yellow) origin, (B) infraspinatus (orange) and supraspinatus (red) origins and (C) deltoid (blue) insertion that were varied in the probabilistic human and chimpanzee models.

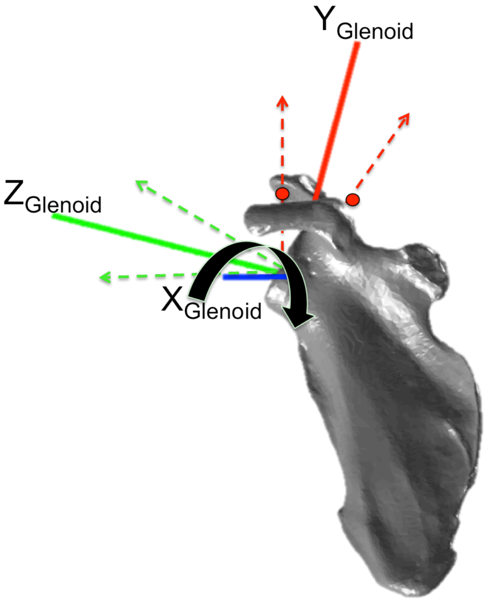


Figure 56: For the probabilistic input of glenoid inclination, the superior point (red dot) of the y-axis of the glenoid coordinate system was shifted mediolaterally to shift the representation of the inclination plane of the glenoid.

Ranges for each input variable were determined through manipulation of the deterministic model, to establish a standard deviation that maintained each variable within reasonable anatomical boundaries of the bones and joints. For muscle insertions and origins, boundaries were estimated on each bone through an iterative process within both the human and chimpanzee model, using values employed in previous, analogous work on humans (Chopp-Hurley, 2015). X, Y and Z coordinates of the rotator cuff origins and deltoid insertion were shifted to determine anatomically realistic variation and standard deviation on the bone surface.

6.4.1.2 Probabilistic Input Variance

The range of variation in glenoid inclination, in degrees, was informed by determining the angular change of inclination associated with each iterative shift of the superior point of the glenoid. Based on this relationship, a standard deviation was determined for the glenoid superior point from previous research on variation of glenoid inclination in human and chimpanzee populations (Chopp-Hurley, 2015; Larson, 1995, 2007). The standard deviation applied to the global mediolateral position of the superior glenoid landmark created an approximately total 20° angular range of glenoid inclination (Table 14) (Larson, 2007).

For stability ratios, no data exists on chimpanzee variability. Differences between species in glenoid stability was determined to be 13.13% in Chapter 5. This difference in stability ratios between the two species was used to guide an appropriate variation for both species. The standard deviation applied to each species represented a total variance of 12% in stability in all eight directions (Table 14).

All standard deviations were kept the same between the two models. This was done to control the effect of the perturbations and avoid the introduction of a confounding factor. The primary outcome of this study was the between species comparison of rotator cuff muscle force predictions. Maintaining the same variability in both models prevented any input from having a greater effect in one model over the other.

Table 14: Means, standard deviations (SD) for all the input variables used in the probabilistic simulations. Insertions and origins means are presented as a percentage of bone length.

	Human	**Chimpanzee**
Input Feature	**Mean (SD)**	**Mean (SD)**
Infraspinatus Origin	**X**: 0.607 (0.035)	**X**: 0.587 (0.035)
	Y: 0.240 (0.035)	**Y**: 0.300 (0.035)
	Z: -0.106 (0.010)	**Z**: -0.200 (0.010)
Subscapularis Origin	**X**: 0.523 (0.035)	**X**: 0.643 (0.035)
	Y: 0.307 (0.035)	**Y**: 0.162 (0.035)
	Z: -0.030 (0.010)	**Z**: -0.0615 (0.010)
Supraspinatus Origin	**X**: 0.360 (0.035)	**X**: 0.460 (0.035)
	Y: 0.315 (0.035)	**Y**: 0.125 (0.035)
	Z: -0.050 (0.010)	**Z**: -0.051 (0.010)
Deltoid Insertion	**X**: 0.369 (0.035)	**X**: 0.346 (0.035)
	Y: -0.004 (0.035)	**Y**: 0.0315 (0.035)
	Z: 0.064 (0.010)	**Z**: 0.0415 (0.010)
Glenoid Inclination (cm)	115.12 (0.3)	104.78 (0.3)
Stability Ratio (%)	0.0 (4.0)	13.13 (4.0)

6.4.1.3 Output Variables of Interest

Using the morphological data ranges for each of the inputs, the geometric module of both the human and chimpanzee model underwent feature alterations of the musculoskeletal features determined from the literature sources. Feature alteration was done through model-based geometric parameter scaling. Outputs from both glenohumeral models were used to construct cumulative distribution functions of specified predicted muscle forces in NESSUS.

To focus the probabilistic analysis, the outputs analyzed were reduced from the deterministic analysis. Notable differences were observed between the human and chimpanzee rotator cuff activation in the Chapter 5 deterministic analysis. These differences likely affect functional capacity at the shoulder, and stochastically exploring them provides greater insight into the full range of shoulder function in both species. Results from Chapter 5 also demonstrated that muscle forces produced in the swing phase of the climb cycle were minimal. To emphasize potential differences between species, the probabilistic analysis was focused on the support phase static instances, where rotator cuff muscle forces were much greater in both species, and thus interspecies differences would be most pronounced.

A total of seven outputs were examined in the three static instances of the climb cycle support phase, representing the entirety of the rotator cuff. Cumulative distribution functions were obtained for the following muscle elements:

- Lower and upper infraspinatus muscle elements
- Lower, middle and upper subscapularis muscle elements
- Supraspinatus
- Teres Minor

6.4.1.4 Sensitivity Factors

Of importance in the present analysis is determination of the effect of each of the input parameters on the output muscle forces. Probabilistic simulations produce absolute and relative sensitivity factors that indicate how the input variables contribute to the distribution of the output variables, normalized to discrete probability level (Laz & Browne, 2010). Relative sensitivity factors are dependent on a reliability index produced in a standard normal variate space of the probabilistic simulation. Monte Carlo simulations do not produce these values, as the simulation is not performed in a standard normalized space, unlike Advance Mean Value. Instead, absolute sensitivity factors can be determined from Monte Carlo simulations. Absolute sensitivity factors can determine how the output variance is affected by both input mean (Equation 14) and standard deviation (Equation 15), and indicate how much the mean and standard deviation of each input affects the output distribution. These values are often averaged across entire locomotion cycles (Laz & Browne, 2010).

Equation 14: Calculation of absolute sensitivity factors for an output distribution from Monte Carlo simulations as determined by perturbation of the mean.

$$S_{\mu} = \frac{\partial p \ \sigma_i}{\partial \mu_i \ p}$$

Equation 15: Calculation of absolute sensitivity factors for an output distribution from Monte Carlo simulations as determined by perturbation of the standard deviation.

$$S_{\sigma} = \frac{\partial p \ \sigma_i}{\partial \sigma_i \ p}$$

For each equation, μ and σ are the mean and standard deviation for a given input variable, and p is the specified probability level. For the purpose of the present study, sensitivity factors of the mean, S_{μ}, will be used to determine the effect of perturbing the mean of each input on the output distributions.

6.4.2 Choosing a Probabilistic Approach

Numerous techniques exist to apply distributions to deterministic equations. The most common, and gold standard is Monte Carlo (Langenderfer et al., 2008). This technique is costly, both in duration and computational capacity. When possible, other more efficient techniques, such as Advance Mean Value (AMV), are employed that use inputs at pre-determined probability levels to predict outputs. AMV uses optimization and reliability to predict a most probable point, which is a combination of model-based parameter values that predict output variables at a specified discrete probability level (Langenderfer et al., 2008). To apply the AMV method, the distributions of the input variables are transformed into independent normal variables. Optimization is then used to locate the most probable point, at which the output values are computed at a desired probability level (Chopp-Hurley, 2015; Wu et al., 1990). AMV has previously been evaluated as an accurate and efficient alternative to the Monte Carlo solution for probabilistic modeling of musculoskeletal systems (Chopp-Hurley, 2015).

As Most Probable Point methods do not calculate discrete solutions repetitively until an entire predicted output variable distribution is constructed, they require a predictable monotonic response model to correctly optimize and predict outputs (Wu et al., 1989). A previous probabilistic analysis using Advance Mean value with human glenohumeral model derived some non-monotonic responses at tails of the probabilistic distribution of some model outputs (Chopp-Hurley, 2015). The present usage challenges both the human and chimp model with kinematic inputs and forces beyond earlier analysis, which could result in similar or worse non-monotonic results.

Therefore, Monte Carlo and Advance Mean Value analyses were run on both the human and chimp model to test the monotonic response of both models. Each Monte Carlo was performed at 2500 iterations to obtain accurate resolution of the resulting cumulative distribution function (Chopp-Hurley, 2015; Langenderfer et al., 2009). Example cumulative distribution functions for one human infraspinatus element output, produced from probabilistic simulations using the input variables from Table 13, are shown in Figure 57. The most probable point method did not always produce comparable cumulative distributions converging with the Monte Carlo. Therefore, the gold standard Monte Carlo was used for all probabilistic analyses.

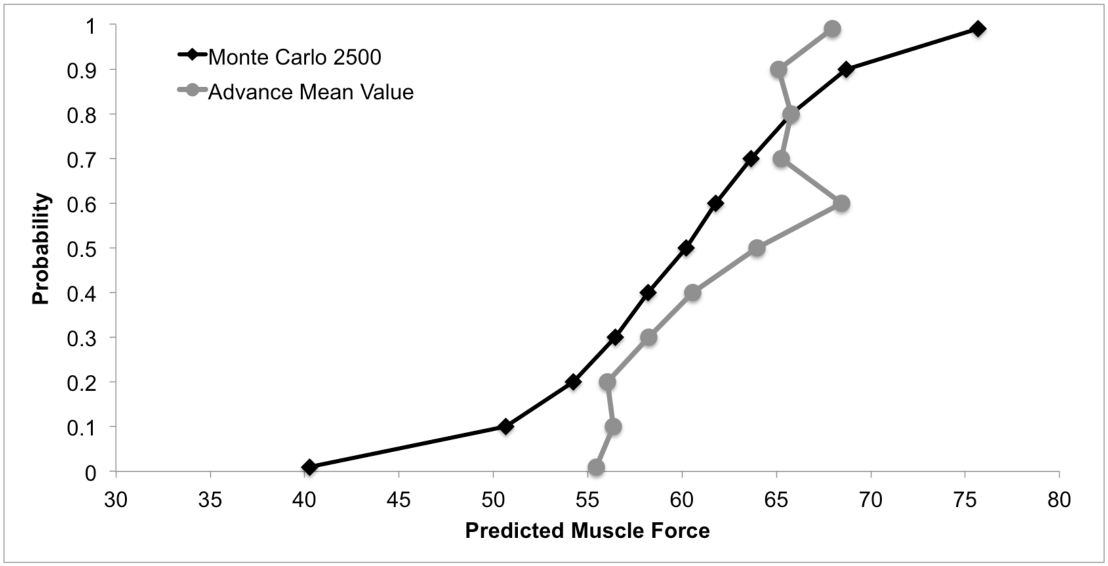


Figure 57: Comparison of Monte Carlo (gold standard) and Advance Mean Value techniques for deriving cumulative probabilistic distributions of predicted muscle force (%). Advance Mean Value did not replicate the results of Monte Carlo and produced non-monotonic points at 0.2, 0.7 and 0.9 probability levels, and inadequate convergence with Monte Carlo at most other levels.

6.4.3 Probabilistic Musculoskeletal Modeling Simulations

The probabilistic model was created by interfacing NESSUS Version 7.01 (Southwest Research Institute) probabilistic analysis software with the Matlab® software used to create the deterministic human and chimpanzee shoulder models. NESSUS software allows the distributions of multiple inputs and model parameters to be applied at once as co-varying variables. Distributions of each of the mentioned morphological features were applied by mapping in NESSUS to the parameters defined within the deterministic model (Chopp-Hurley, 2015). This process created distributions for the desired output variables.

To create a probabilistic model, the geometric module was altered in both the chimpanzee and human models to have the mean value of each input feature in the original deterministic models. Means and standard deviations of each of the input variables (Table 15) were set in NESSUS for both the human and chimpanzee models and used to form a normal (Gaussian) distribution for each morphological variable. Normal distributions were selected, as they are the most commonly used in science and engineering, and typically best represent the true distribution of biological phenomena (Choi et al., 2007; Langenderfer et al., 2009). Each of these variables was then mapped to the line of code in the MATLAB glenohumeral model program representing the mean value. All input variables were perturbed simultaneously in NESSUS. By assessing all morphological variables at once, the simultaneous effect of all feature's variability on rotator cuff muscle forces was determined, allowing for interaction between input variables.

6.4.3.1 Probabilistic Simulations

The human and chimpanzee model were examined with the same kinematic climbing inputs used in Chapter 3 Study 1, using the distributional inputs for all 14 features in Table 15 through a NESSUS interfacing.

A series of Monte Carlo simulations were run at 2500 iterations for each of the output normalized muscle forces, in the three static support instances of early, mid and late support, for both the human and chimpanzee glenohumeral model. A 2500 iteration Monte Carlo has been shown to sufficiently convergence on the correct solution (Chopp-Hurley, 2015; Langenderfer et al., 2009). A total of 42 Monte Carlo simulations were completed. Each Monte Carlo created a cumulative distribution function, with probabilities at 11 specified levels – 0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 0.99 – and sensitivity factors for each of the input parameters at each probability level.

6.4.3.2 Covariance

Musculoskeletal features may co-vary. The human body is a connected system. A change in one feature may have an expected associated change in a related musculoskeletal feature. The chosen probabilistic approach allows the full range of each input distribution to be considered in combination with the full range of all other input feature distributions. This means that combinations of features may be considered that are not necessarily biologically realistic. However, the influence of covariance for several morphological shoulder features on subacromial geometry was determined to be very low (Chopp-Hurley, 2015). For this reason, covariance was assumed to be negligible in the present study and not incorporated into the model.

6.5 Data Analysis

Human and chimpanzee muscle forces of the rotator cuff (supraspinatus, infraspinatus, subscapularis, teres minor) from the three static support instances (early, mid and late) were analyzed as outputs of the probabilistic Monte Carlo analysis in NESSUS. The 1st (minimum), 50th (median) and 99th (maximum) probability levels were extracted from resultant cumulative distribution functions to compare predicted 99% confidence interval ranges of muscle forces between chimpanzees and humans. Overlap in confidence intervals of chimpanzees and humans determined whether there was quantitative convergence in rotator cuff muscle forces between species.

To test the relationship between each morphological feature and the outputs, sensitivity factors were extrapolated from each of the Monte Carlo analyses. Sensitivity factors were produced for each of the input variables, at each of the 11 discrete probability levels (0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 0.99) for each Monte Carlo analysis on each of the seven output variables, for all three static support instances. As each sensitivity factor is normalized to their probability level, the factors were averaged across the probability levels and then across each of the instances of the climb cycle support phase (Laz & Browne, 2010). The final sensitivity factors represent the averaged effect of 14 input variables to each of the seven output variables.

6.6 Results

Resulting cumulative distribution functions were used to determine overlap and convergence between species in rotator cuff muscle force distributions. The 50th percentile of the cumulative distribution for each output muscle force is represented by bar height, while the error bars indicate the 1st and 99th percentiles, representing a 99% confidence interval (Figure 58).

6.6.1 Muscle Force Distributions

Differences in muscle forces between species that existed in the deterministic model persisted in the probabilistic simulation. Most muscle activity was in early and mid support. The confidence intervals of late support rotator cuff muscle activity were low for both species models, with all intervals falling within [range 0 – 8]% maximal force. Resultantly, the late support confidence intervals for all rotator cuff muscles for both the chimpanzee and human models were overlapping (Figure 58).

Predictions for the human rotator cuff muscles of infraspinatus and teres minor were much greater than the chimpanzee, with predictions near 100% muscle force being possible in early and mid support instances (Figure 58). The confidence intervals for the human upper and lower infraspinatus, and teres minor in early support had mean values of 0[range 0 – 100]%, 77.71[range 0 – 100]% and 62.48[range 0 – 100]%, respectively. Due to these large confidence intervals, they overlapped with the predicted range of forces for respective chimpanzee muscles, despite the chimpanzee confidence intervals being much lower (Figure 58).

As was seen in the deterministic analysis, only chimpanzees were predicted to activate the subscapularis and supraspinatus muscles in most of support phase. Activation of subscapularis was mostly restricted to the upper element in chimpanzees in early, 5.72[range 0 – 57.71]%, and mid support, 23.51[range 17.82 – 28.51]%. Human subscapularis activity was low, and mostly in late support (Figure

58). A small bout of subscapularis activity occurred in the lower element, though the mean was 0[range 0 – 6.31]%. Similarly, the only human supraspinatus activity confidence interval that was non-zero was in late support and was very low, with a mean of 0[range 0 – 6.24]%. Chimpanzees had consistent, but low, activity from supraspinatus throughout the support phase (Figure 58).

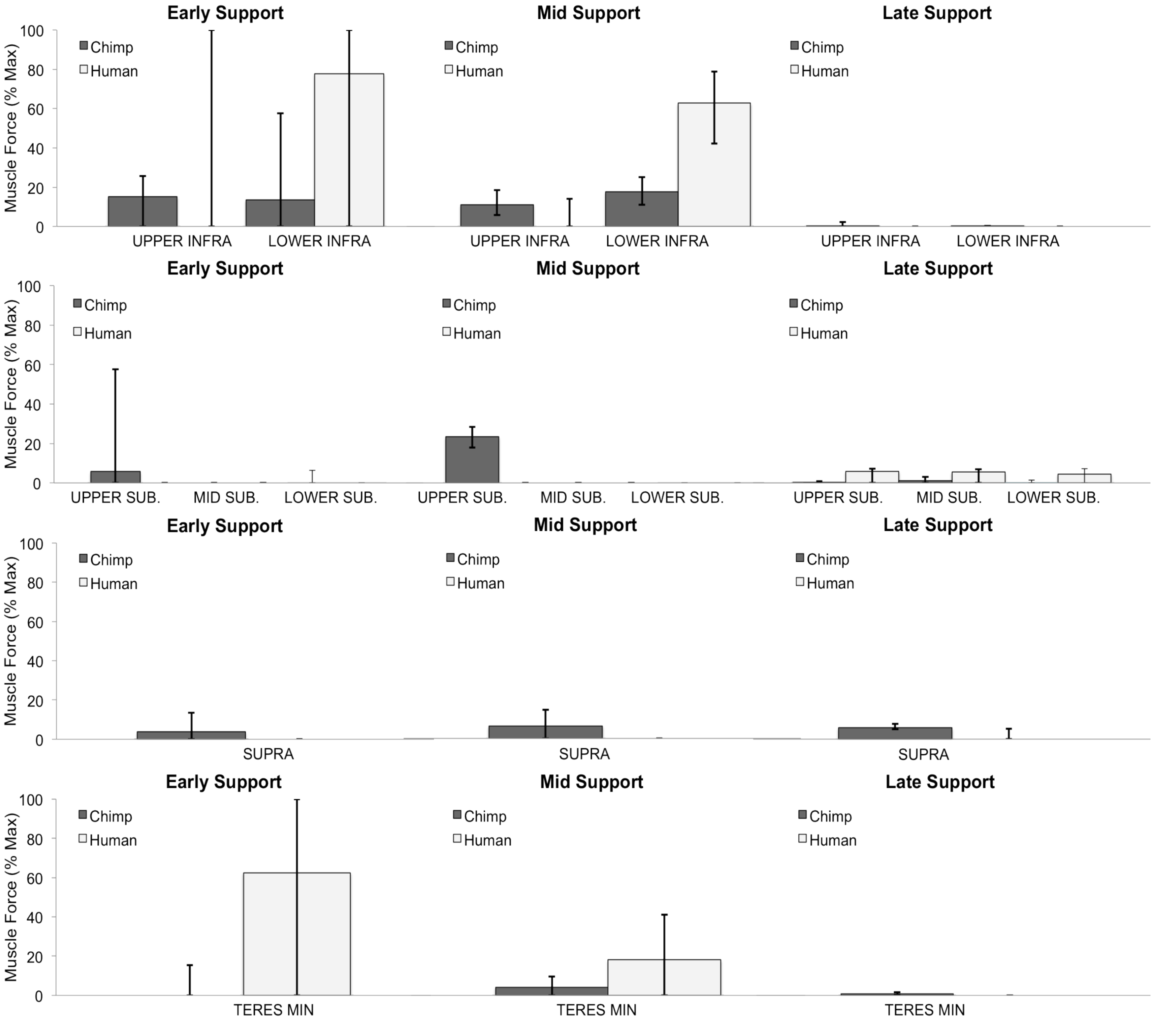


Figure 58: Results of the Monte Carlo analysis for all four rotator cuff muscles. Results are shown for the three static instances of the support phase of the climb cycle. Bars represent the 50th percentile. Error bars represent the 99% confidence interval.

6.6.2 Sensitivity Factors

Averaged muscle force sensitivity factors to each of the inputs are presented in Figure 59. Results from sensitivity factors demonstrated Greater values indicate a greater effect of perturbing the mean of the specific input on the resultant output variable distribution. The inputs with the greatest effect differed between the two species models. The anterior-posterior perturbation along the z-component of subscapularis origin consistently had the greatest sensitivity factor in humans. Other factors that had a greater effect included the anterioposterior z-component of the supraspinatus insertion on the scapula, y- (anterioposterior) and z-component (mediolateral) of the deltoid insertion on the humerus. The infraspinatus y- and z-component and supraspinatus y-component also had a notable effect on some of the rotator cuff element distributions (Figure 59).

All the sensitivity factors with the greatest effect on the outputs in humans were among the most notable in the chimpanzee model as well. However, the effect of each was not the same as the human model (Figure 59). The deltoid z-component (representing mediolateral perturbations) had the greatest overall effect on all the chimpanzee rotator cuff outputs (Figure 59). The y-component (mediolateral perturbations) and z-component (anterioposterior perturbations) of infraspinatus, subscapularis, and supraspinatus origins, and the y-component (anterioposterior perturbations) of the deltoid insertion were also among some of the inputs with the greatest impact on the chimpanzee output muscle force distributions.

Changes to glenoid inclination and stability ratios had a negligible effect on the output distributions (Figure 59). The x-components of all the muscle insertions and origins – representing perturbations along the length of the scapula and humerus – had a smaller effect than the y- and z-components.

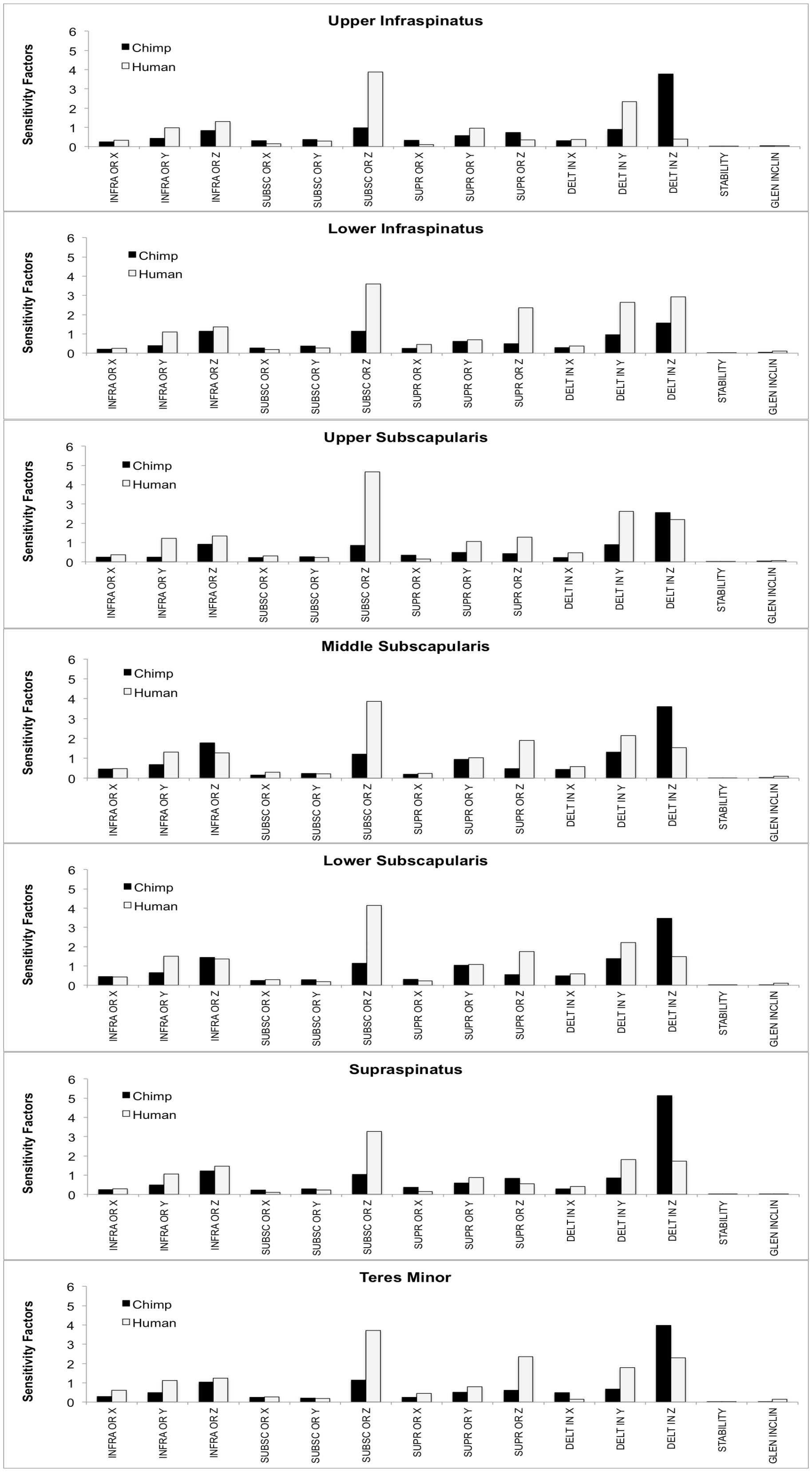


Figure 59: Sensitivity factor of each of the seven output muscle elements to perturbations of the input variables.

6.7 Discussion

The present probabilistic modeling of the chimpanzee and human glenohumeral joint permits population level comparisons between the two closely related species. Not only does this research indicate whether functional overlap can occur between the two species, it also identifies morphological features that affect function, substantiates previous evolutionary morphometric comparisons and implicates evolutionary adaptations in the development of glenohumeral musculoskeletal disorders.

Hypothesis one was mostly not supported. Muscles that were predicted to not contribute to the climbing task deterministically were also predicted to not contribute stochastically. In particular, the probabilistic simulations still limited observed human model rotator cuff muscle activity to infraspinatus and teres minor. While large distributions were produced for infraspinatus and teres minor, causing overlap between chimpanzees and humans in these two muscle forces, no species convergence existed for subscapularis or supraspinatus muscle force distribution. While perturbations of rotator cuff muscle origins on the scapula contributed to resultant infraspinatus and teres minor muscle force distributions, glenoid inclination had a negligible effect on

Hypothesis two was partially supported for the chimpanzee model only. The sensitivity factors indicate that the deltoid z-component, representing medial-lateral shifts to the insertion of the muscle, had the greatest effect on the distribution of the supraspinatus muscle force in the chimpanzee model. While the deltoid z- and y-components did have an effect on the supraspinatus muscle force distribution in humans, the supraspinatus muscle force output remained zero, except in late support.

Hypothesis three was not supported. Perturbations of the stability ratios had an insignificant effect on all the rotator cuff output distributions

6.7.1 Probabilistic Simulation Methods

Many probabilistic methods exist to determine distributions of biological phenomena. While Monte Carlo is considered the gold standard, Most Probable Point Methods such as Advance Mean Value (AMV) are much more efficient (Laz & Browne, 2010). AMV defines the performance function based on a small number of adjustments about the input mean values. The resultant cumulative distribution is dependent on the how those initial adjustments define the performance function (Wu et al., 1989). Therefore, AMV relies on the performance function being perturbed behaving monotonically to estimate the cumulative distribution function (Wu et al., 1989). If the performance function has many variables, or does not behave in a systemic manner, the performance function will struggle to converge on the correct cumulative distribution function. The eventual choice of probabilistic method is dependent on the problem being simulated.

While the efficiency of Advance Mean Value made it an appealing method, the gold standard Monte Carlo was employed for the current study. In initial probabilistic piloting assessments, AMV did not converge with Monte Carlo simulations for numerous output cumulative distributions, unlike previous work that applied the AMV technique to probabilistic simulations of the SLAM model (Chopp-Hurley, 2015). While this was mostly successful, non-monotonic performance was also reported with AMV techniques, in which Monte Carlo was the more reliable technique (Chopp-Hurley, 2015). The complexity of the multistep functions within both the chimpanzee and human model likely reduced the predicative ability of AMV. Caution should be exercised when attempting to apply AMV to multi-function computational models with a high number of variables that are transformed repeatedly until their final iteration for output calculation. Though costly, both in computation and time, Monte Carlo methods produce the most reliable cumulative distribution functions (Wu et al., 1989).

6.7.2 Species Probabilistic Differences

Human muscle forces remained different than chimpanzees, and higher, denoting the difficulty of the climbing task. The human infraspinatus and teres minor activated as high as 100% of muscle force within the 99% confidence interval. Corresponding chimpanzee confidence intervals were typically below 40% maximal force. That the human model can predict up to maximal force demonstrates the difficulty of the task for the human glenohumeral joint, specifically as represented in SLAM. Though possibly ancestral, weight-bearing horizontal bimanual arm-suspension climbing places the modern human glenohumeral joint under immense duress, requiring high muscle forces as a percentage of maximal force producing capabilities to counter external forces (Lewis et al., 2001). Increasing the intrinsic stability of the joint, and thus decreasing the muscle force necessary to counter shearing forces at the joint, did not appear to ease task completion markedly for the human model. Similarly, shifting the inclination of the glenoid, insertions of the rotator cuff muscles or the insertion of the deltoid did not noticeably decrease the difficulty of climbing for humans or improve force sharing across all rotator cuff muscles, indicating a robustness of this extreme demand.

The perturbed geometric features were selected because they are considered evolutionarily relevant to arboreal and brachiation locomotion. Probabilistic modeling of the deltoid insertion on the humerus represents a change to the position of the deltoid tuberosity. Change in the placement of this boney feature is hypothesized to affect the leverage of the deltoids and contribution of the deltoids to climbing (Ashton & Oxnard, 1963; Larson, 1995, 1998). The stochastic modeling of the glenoid inclination and rotator cuff origins aimed to reflect boney changes to the scapular body and glenohumeral joint orientation. Glenoid superior-inferior inclination affects the orientation of the glenohumeral joint. The superior orientation of the chimpanzee glenoid optimizes the entire glenohumeral joint for overhead behaviors by opening the joint up to elevated arm positions and aligning muscle fibers and lines of action for overhead, climbing behaviors (Larson, 1998; Lewis et al., 2001). Shifting the position of the infraspinatus, subscapularis and supraspinatus insertions on the scapular body represented shifts to the shape of the scapular body. The chimpanzee scapular body is longer and less wide than the human, hypothetically due to the superior direction of the forces exerted by the muscles originating on the scapular body (Larson, 1995, 2015; Larson & Stern, 2013). The stability ratios represent the intrinsic difference between chimpanzees and humans in capacity of the glenoid to withstand dislocating external forces (Lippitt et al., 1993). The deeper chimpanzee glenoid provides more intrinsic stability, which requires less muscle force to counter moments occurring about the joint (Matsen et al., 1994).

The effect of all the morphological perturbations was not enough to substantially shift the human rotator cuff muscle forces toward convergence with the chimpanzee model outputs. The human supraspinatus and subscapularis were not predicted to have distributions similar to chimpanzees. While the chimpanzee distributions for infraspinatus and teres minor fell within those of the human, this was primarily because the human distributions represented the entire range of possible muscle force values. The chimpanzee distributions for infraspinatus and teres minor were much smaller than the human distributions. The most noticeable effect of the geometric perturbations was the very wide confidence intervals of the human infraspinatus and teres minor. These confidence intervals seem to implicate a narrow range of possible changes with evolutionary morphological perturbations. Instead of converging on more chimpanzee like behaviors, the human stochastic model trended toward overloading the infraspinatus and teres minor. This suggests none of present probabilistic modeling choices modified the human shoulder toward ancestral abilities or lessened the burden of climbing on the modern human shoulder. For climbing to be considered a feasible task for modern humans, evolutionary changes beyond those examined the present study must be considered.

Human rotator cuff muscle force distributions were mostly restricted to infraspinatus and teres minor. This may denote the importance of these muscles to climbing and weight-bearing activities. As a percentage of the total rotator cuff physiological cross sectional area (PCSA), the human infraspinatus and teres minor constitute a larger percentage of total rotator cuff physiological cross sectional area than in other primates (Mathewson et al., 2014; Thorpe et al., 1999). While these differences from other primates are no more than 9% of the total cuff PCSA, they may influence the congruous contribution of the rotator cuff to upper extremity tasks. The human rotator cuff, while overall very similar to the chimpanzee, is more infraspinatus dominant (Sonneband et al., 2009). The teres minor still constitutes the smallest rotator cuff muscle, but has a greater PCSA in humans than other primates (Carlson, 2006; Mathewson et al., 2014; Thorpe et al., 1999). Infraspinatus and teres minor are hypothesized to have similar roles in horizontal bimanual arm-swing. Both muscles are highly active in chimpanzees during the support phase of climbing, more so than supraspinatus or subscapularis (Larson & Stern, 2013). The increase in size as a proportion of the total rotator cuff of both infraspinatus and teres minor in humans may explain their greater dominance in the computational human model.

Subscapularis and supraspinatus were rarely predicted to be active in the human model during support phase of the climb cycle. No shifts in the inputs, particularly muscle insertions, shifted the geometry to increase the probability of activation of either supraspinatus or subscapularis. While subscapularis is not considered a highly active muscle during climbing support phase, this outcome was surprising for supraspinatus. Supraspinatus in chimpanzees has an important role in climbing as a joint stabilizer and arm elevator (Larson et al., 1992, 1989). Supraspinatus is active at low levels in chimpanzees during the climbing support phase (Larson, 1986; Larson & Stern, 2013). The lack of activity in the human model may signify the decreasing evolutionary role of supraspinatus in the human glenohumeral joint. Along with subscapularis, supraspinatus has a modest PCSA as a percentage of total rotator cuff PCSA, and the size of the muscle is closer to that of a rabbit (Figure 60) (Mathewson et al., 2014). This may relate to the need to reduce the size of the muscle to accommodate the narrower subacromial space the supraspinatus tendon passes through in humans (Voisin et al., 2014). Resultantly, the supraspinatus is a weaker muscle with a less prominent role at the glenohumeral joint. The deltoids have a much greater volume and PCSA at the glenohumeral joint in humans, proportionally to the rotator cuff, compared to other primates (Carlson, 2006; Thorpe et al., 1999). This creates less of a role for the supraspinatus in arm elevation (Santago et al., 2015). Supraspinatus is also considered an important joint stabilizer (Larson & Stern, 1992). However, to counter the superior, elevating action of the deltoids, the computational model optimization routine would select a mathematically stronger muscle that could geometrically perform a similar stabilizing role, such as infraspinatus.

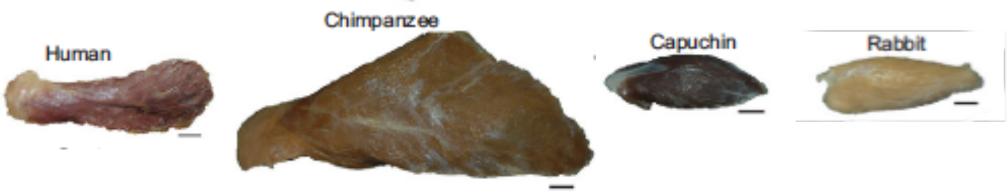


Figure 60: Comparison of muscle size of the supraspinatus between a human (73.41kg), chimpanzee (40.90kg), capuchin monkey (3.97kg) and rabbit (3.16kg). Scale bar represents 10mm. The human suprapinatus is more comparable in size to much smaller animals. From Mathewson et al., 2014.

The width of the human infraspinatus and teres minor confidence intervals indicates an exchange between minimizing and overloading each of the muscles. It was expected that perturbation of the morphologcal inputs would result in greater force sharing, similar to that predicted in the chimpanzee model. Rather, the human model remained exclusive to infraspinatus and teres minor activity, with confidence intervals that included the entire breadth of possible muscle forces. This suggests that the human shoulder model was only capable of distributing the necessary muscle force between infraspinatus and teres minor with the performed input perturbations, likely due to muscle rotational contributions. This offloading would not be an effective mechanism for improving climbing strategies and performance in humans. In reducing the muscle force of either infraspinatus or teres minor, the model appears to shift any carryover muscle force to an already highly active muscle. Many muscles at the human shoulder have low force producing capabilities and lines of action that are not optimized for overhead tasks (Carlson, 2006; Larson & Stern, 2013; Lewis et al., 2001). This prevents other glenohumeral muscles from being feasible alternatives to offload the infraspinatus or teres minor muscles. Despite muscle redundancy, these results suggest the human shoulder is reliant on a narrow set of muscles for overhead behaviors. The apparent inability to shift loads to alternate glenohumeral muscles in the modern human shoulder indicates a lack of mechanisms to prevent muscle overload and early-onset fatigue.

6.7.3 Output Sensitivity to Input Perturbation

Perturbations to muscle insertions and origins had the greatest effect on resultant rotator cuff muscle forces. In physical anthropology, muscle fiber orientation, muscle line of action, and joint orientation is often associated with bone shape (Green, 2013; Larson, 2015). Changes to muscle origins and insertions affect the orientation of muscle fibers as they cross the joint (Larson & Stern, 2013). While muscle attachments positions were strong modifiers of muscle force outputs, they did not cause distributions that indicated that humans could converge toward chimpanzee glenohumeral biomechanics. Rather, they reinforced existing biomechanical patterns in each species. Humans maintained selection bias for infraspinatus and teres minor only. These results limit the inference that modest perturbations to muscle origins and insertions are strongly associated with evolutionary species-specific function and locomotion. Recently, scapular shape association with rotator cuff muscle function and locomotor behavior has been questioned (Larson & Stern, 2013). Supraspinatus, infraspinatus and subscapularis fossae size do not correlate well to muscle size, and locomotor behaviors across primate species (Larson & Stern, 2013). Limited correlation between fossae and muscle size may also extend to other bones such as the humerus. As isolated features, rotator cuff muscle origin and insertion sites do modestly affect within-species muscle force sharing strategies, but do not strongly affect functional behavioral outcomes such as bimanual climbing capacity.

All outputs were less sensitive to shifts in the insertions and origins of muscles along the long axis of the scapula and humerus (x-components). The chimpanzee scapula is longer and narrower than the human scapula, and mediolaterally compressed (Figure 61) (Hunt, 1991). This has elongated the size of the infraspinatus and subscapularis fossae (Green et al., 2015; Larson, 2015). This is hypothesized to affect the size of muscles originating on these fossae, and muscle fiber orientation (Figure 61) (Larson & Stern, 2013). The superior-inferior position of the deltoid insertion is a distinguishing trait between humans and chimpanzees (Larson, 1998) and is hypothesized to change the leverage of the deltoids, and force sharing with the rotator cuff. Perturbing the origins and insertions of either the human or chimpanzee along the length of the scapula or humerus did not greatly affect the predicted muscle forces and rotator cuff force sharing compared to medial-lateral and anterior-posterior perturbations. Therefore, changes to human muscle positions that can elongate muscle lines of action in a superior orientation are not highly likely to produce chimpanzee-like muscle forces.

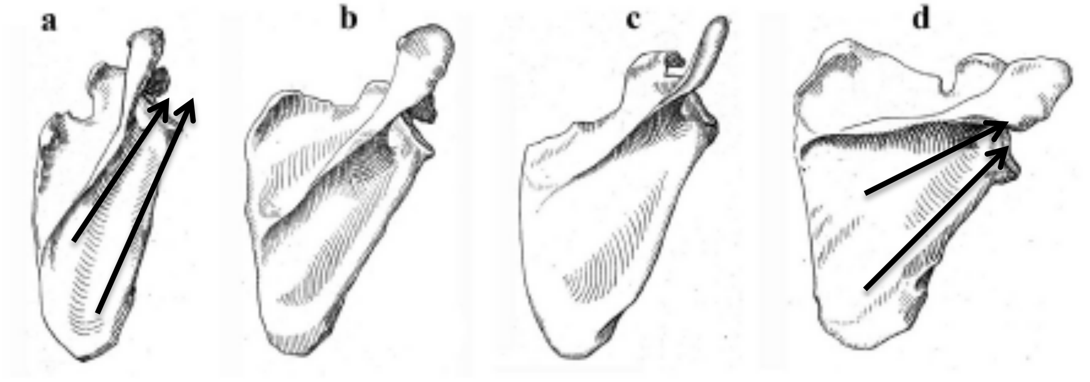


Figure 61: Comparison of the chimpanzee (a), gorilla (b), orangutan (c) and human (d) scapular shape, and glenoid and scapular spine orientation. Infraspinatus lines of action are shown on the chimpanzee and human scapulae. From Voisin et al., 2014.

None of the output muscle forces were sensitive to perturbations of glenoid inclination. Glenoid inclination is associated with upper extremity utility, as a superior inclination exists in suspensory primates like chimpanzees (Green, 2013; Larson, 2008; Lewis et al., 2001). Present results may be due to the implemented variation in inclination not being large enough to affect change in muscle force sharing. However, it is also possible that shifts in solely inclination may not produce noticeable effects without other concurrent physical form shifts at the joint.

Inclination alone will not necessarily reposition the joint in a manner that brings about associated changes to muscle force distributions. To mimic the 'shrugged' chimpanzee glenohumeral joint that is optimized for more overhead postures, the human glenoid would need a more superior inclination and the entire glenohumeral joint to be translated superiorly (Figure 61) (Larson & Stern, 2013; Voisin et al., 2014). Inclination variability alone will include opening the glenohumeral joint superiorly, but will not superiorly raise the joint like the chimpanzee (Figure 61). Further, without the concurrent superior reorientation of the scapular spine and acromion, it is unlikely that the muscle lines of action will change markedly and distinguish locomotor behaviors between species (Figure 61) (Ashton & Oxnard, 1964; Green, 2013; Larson & Stern, 2013).

Stability ratios did not have a notable effect on any of the muscle force outputs for either the human or chimpanzee model. Previous stochastic research involving the human shoulder model, SLAM, similarly found stability ratios to have a minimal contribution to muscle force output distributions (Chopp-Hurley et al., 2014). The variability attributed to the stability ratios was smaller in the present study, as they were modified to a range that represented the difference between humans and chimpanzees. Muscle origins and insertions had a much greater effect on rotator cuff muscle force distributions.

The human and chimpanzee models had different sensitivities to the probabilistic inputs. Despite being a fairly inactive muscle, the human model was most sensitive to perturbations of the subscapularis z-component (anterior-posterior shifts), while the chimpanzee model was most sensitive to the deltoid z-component (medial-lateral shifts). The two models were designed to be analogous, except for the geometric module where bone and muscle geometry diverge. The difference in sensitivity is likely a response to species differences in force sharing due to differences in muscle biomechanics and physiological properties across the glenohumeral joint. Chimpanzees have a larger rotator cuff PCSA and size relative to the deltoid muscles than humans (Carlson, 2006; Thorpe et al., 1999). This increases the capacity of the rotator cuff to contribute to weight-bearing tasks like climbing

(Santago et al., 2015). In turn, greater force sharing and exchange is possible between the rotator cuff and deltoids. For this reason, modifying the deltoid insertion in the medial-lateral direction likely alters the contribution of the rotator cuff to glenohumeral joint muscle moment. The sensitivity of all outputs to subscapularis origin medial-lateral position is less clear. Subscapularis is not considered an important contributor to bimanual climbing support phase beyond axial rotation in late support (Larson et al., 1986). However, all muscles have interdependent roles at the glenohumeral joint and subscapularis has been previously shown to contribute to numerous rotator cuff muscle force distributions in probabilistic modeling of the human SLAM model (Chopp-Hurley et al., 2014). Though not predicted to be very active in support phase, the geometry of subscapularis may still influence the eventual compensations of other rotator cuff muscles to glenohumeral stability. This may be more pronounced in humans due to the reduced force producing capacity of the rotator cuff muscles (Mathewson et al., 2014).

6.7.4 Implications for Modern Glenohumeral Function

The action of the rotator cuff and deltoid muscles is similar between chimpanzees and humans, with some key evolutionary adaptations that have altered force sharing about the glenohumeral joint. The rotator cuff and deltoids have been emphasized as force couples that provide synergistic stabilization to the glenohumeral joint for a versatile set of behaviors (Inman et al., 1944). However, in chimpanzees and other primates, this role may be secondary to active weight-bearing locomotor roles (Larson et al., 1986; Roberts, 1974). Upper extremity locomotor differences between primates and humans are emphasized by evolutionary divergence in musculoskeletal form (Larson, 1998). The human rotator cuff is smaller in size and absolute PCSA than the chimpanzee (Carlson, 2006). The human deltoids, however, have remained large proportionally to the rotator cuff (Carlson, 2006). Owing to non-weight-bearing usage, the human rotator cuff is smaller. This proposed evolutionary adaptation lowers segment masses and accommodates boney changes such as a laterally projecting acromion that has narrowed the subacromial space through which the supraspinatus passes (Voisin et al., 2014; Wood & Richmond, 2001). In particular, subscapularis and supraspinatus have reduced in size and PCSA as a proportion of the rotator cuff, placing more responsibility on the infraspinatus (Mathewson et al., 2014). This has resulted in evolutionary changes to the force-sharing relationship between the rotator cuff and deltoids in humans. As force couples compressing the humeral head into the glenoid, the modern human rotator cuff is highly reliant on the infraspinatus to counter the superior pull of the deltoids (Figure 62). This difference was highlighted by the computational comparison of the chimpanzee and human glenohumeral models for a horizontal bimanual arm-suspension climbing task. The human model predicted high infraspinatus and teres minor muscle forces coupled with deltoid action, while the chimpanzee model predicted moderate infraspinatus forces with accompanying force from all other rotator cuff muscles.

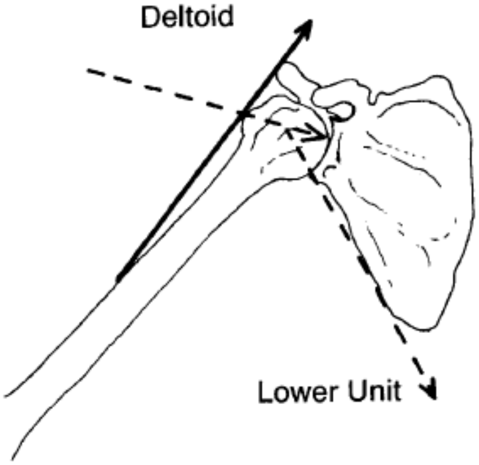


Figure 62: Force coupling of the deltoid and rotator cuff about the glenohumeral joint centering the humeral head in the glenoid. In humans, the superior pull of the larger deltoids is much greater than the inferior pull of the lower muscle unit that comprises the much smaller rotator cuff muscles.

The divergent force sharing relationship of the rotator cuff muscles between humans and chimpanzees was not reduced through probabilistic techniques employed in the current study. Perturbing physical features linked to evolutionarily relevant upper extremity, overhead behaviors in chimpanzee and human computational models was expected to affect the role of individual upper extremity muscles, and possibly cause convergence between the two species. The human model maintained infraspinatus and teres minor dominance, and the resultant distributions highlighted the high potential for overload of these two muscles in bimanual climbing. None of the morphological inputs caused activation of supraspinatus or subscapularis in the human model and greater muscle recruitment across more rotator cuff muscles in the human model. The modern human glenohumeral joint is more reliant on the infraspinatus muscle than other primates to provide axial rotation, adduction and joint stability (Mathewson et al, 2014). Consequently, the infraspinatus muscle is susceptible to overload in overhead tasks. Infraspinatus fatigue initiates a sequence of biomechanical events that lead to subacromial impingement and rotator cuff injury (Borstad et al., 2009; Ebaugh et al., 2006). Reliance on infraspinatus, despite variation of evolutionarily significant musculoskeletal features, highlights the low efficacy of the modern human glenohumeral joint in overhead, weight-bearing activities.

The diminished role of supraspinatus and subscapularis in human bimanual climbing shoulder function is likely rooted in evolutionary shifts away from locomotor behaviors that implicate the upper extremity. The human rotator cuff remains subscapularis dominant likely due to evolutionary relation to primates and ancient weight-bearing locomotor patterns. Primates are subscapularis dominant due to an increased need for axial rotation in the upper limb (Mathewson et al., 2014). Unlike habitual terrestrial quadrupedal mammals whose locomotion occurs mostly in the sagittal plane, primate locomotion is variable and, thus, multi-planar (Larson et al., 1986). Hand placement during suspensory climbing is extremely important and variable, and requires a large degree of internal rotation (Larson et al., 1986; Stern & Larson, 2001). This necessitates an important contribution from subscapularis to locomotion behaviors in primates. Similarly, the supraspinatus is important for primates to provide synergistic stability over a larger range of motion than terrestrial mammals, and to abduct the arm into overhead postures only assumed in primates (Mathewson et al., 2014; Tuttle & Basmajian, 1978). As humans devolved locomotor usage of their upper extremity, the shoulder form reorganized toward non-weight-bearing, below shoulder-height behaviors such as throwing, carrying and tool manipulation (Bramble & Lieberman, 2004; Roach et al., 2013). The acromion became more laterally projected to increase the deltoid leverage in below shoulder movements, reducing the subacromial space (Voisin et al., 2014; Potau et al., 2007). Subscapularis and supraspinatus became engaged in fewer high force tasks, which no longer required muscles with large force producing capabilities (Potau et al., 2007). Rather, both muscles remain important synergists in modern behaviors such as push and pull tasks, and those involving below-shoulder-height axial rotation (Lee et al., 2000; McDonald et al., 2012). While the role of these muscles has diminished in ancestral behaviors, they remain dominant in typical human lifestyle and occupational tasks.

The present results highlight the root of increased subacromial and rotator cuff injury risk in modern humans in the context of evolutionary changes to the shoulder. The modern human shoulder musculoskeletal form has numerous, unique benefits, but also incurs species-specific injury risks. Subacromial impingement syndrome is one of the most common disorders of the human shoulder (Van der Windt et al. 1995). This disorder is believed to arise from rotator cuff fatigue creating an imbalance in the stabilizing muscle forces about the glenohumeral joint (Lewis et al., 2001; Rashedi et al., 2014). Rotator cuff muscles, particularly the supraspinatus and infraspinatus, resist the superior pull of the deltoids that act to elevate the arm and translate the humeral head in the glenoid (Howell et al. 1986; Roberts, 1974; Thompson et al. 1996). The evolutionarily reduced size of supraspinatus reduces the muscle mechanisms available to resist the superior translation of the humeral head with deltoid activation. Combined with the reduced size and absolute PCSA of all rotator cuff muscles, and deltoids that have remained large and strong, the rotator cuff muscles become fatigued easily when resisting the action of the deltoids in overhead postures (Ebaugh et al., 2006; Sood et al., 2007). Once the rotator cuff is fatigued, the deltoids superiorly translate the humeral head with less resistance, decreasing the subacromial space (Chopp et al., 2011). As humans already have an evolutionarily smaller subacromial space, the supraspinatus tendon becomes impinged. The result is an evolved propensity in humans for subacromial impingement and rotator cuff tears.

This result has implications for modern work place settings where repetitive, overhead tasks are common. The bimanual climbing task analyzed is not a typical, modern occupational, or even recreational task. It does, however, provide an evolutionary example of the response of the human musculoskeletal system to more extreme and evolutionarily relevant shoulder exposures. Occupational biomechanics research has demonstrated the risk for shoulder pain and injury from repetitive overhead postures, with muscle fatigue often implicated as the mitigating factor (Ebaugh et al., 2006; Nussbaum et al., 2001; Sood et al., 2007). Synergistic muscle imbalances can also occur in overhead postures as muscle lines of action become augmented, compromising glenohumeral joint stability (Lee et al., 2000). The more taxing bimanual climbing task mirrored the research of occupational biomechanics by demonstrating a likely scenario for rapid rotator cuff fatigue, particularly of the infraspinatus. The analysis also demonstrated the mechanical compromise of supraspinatus and subscapularis in overhead postures. The lack of convergence with chimpanzee muscular function in the present probabilistic simulation reiterated how strongly entrenched this injury mechanism is in modern human shoulder structure.

Though it did not bring about functional convergence between the two species in the present study, muscle origins and insertions strongly influence specific muscle function. Muscle attachment positions were the most important input predictors of rotator cuff muscle force distributions, but were not always most important for corresponding muscle forces – each input muscle position had an affect on numerous output muscle forces. Muscle size and configuration of different species and fossils is often surmised from bone shape in comparative morphometric analyses in physical anthropology (Hutchinson, 2012). This association is not always strong, however, as physiological and biomechanical data is often lost in osteological analyses (Bello-Hellegouarch et al., 2013; Larson, 2015). The most important resultant effect of changes to bone shape and size is the reconfiguration of joint orientations for muscle lines of action and moment arms (Biewener, 1990). Results of the present study support previous work, as shifting muscle lines of action had the greatest effect on biomechanical muscle force sharing about the glenohumeral joint. Perturbation of a muscle insertion or origin did not necessarily have the greatest effect on its own muscle force distribution over perturbations of other muscle insertions and origins. This outcome is likely indicative of the muscle force sharing responsibility in glenohumeral muscles to provide synergistic stability about the joint.

6.7.5 Limitations

There are limitations to using probabilistic modeling to infer biological phenomena. First, the probabilistic model depends the biological realism of the deterministic model. Some predictions in both present models do not fully replicate experimentally measured muscle activity. The chimpanzee model was purposely designed to parallel the pre-existing human model for direct comparisons between species. Differences between the two deterministic models are due to differences in musculoskeletal geometry. While the differences between the two species in each model may not perfectly reflect biological reality, due to the similar structure of both models, the differences in muscle force outputs do reflect computational biomechanical differences. These results can be used to infer differences in biomechanical function. Future analyses could consider modifications to the optimization routine in both models, such as co-activation constraints, to improve predictions of muscle force couples. Second, probabilistic modeling is dependent on the input and output variables. Only a select few evolutionarily inputs were considered. Numerous other glenohumeral musculoskeletal features have been associated with function. These include rotator cuff insertions on the humeral head, deltoid origins on the clavicle and scapula, muscle PCSA, scapular spine orientation, acromion shape, glenoid shape (Larson, 1995; Larson et al., 1986, Mathewson et al., 2014; Voisin et al., 2014). Inclusion of these inputs may have prompted more convergence between species in muscle force distributions. Further, due to methodological constraints, only rotator cuff muscle distributions were analyzed in the probabilistic analysis. It is possible the inputs influenced the behaviors of other muscles not considered, such as the deltoids, and other geometric features such as subacromial space. Future work should consider the analysis of other evolutionarily relevant shoulder muscle groups.

The lack of effect of some input variables may be due to the variation used, or not including highly associated musculoskeletal features in the probabilistic analysis. Moderate standard deviations were applied to all input variables. Some of variations were less than those used in previous probabilistic analysis (Chopp-Hurley, 2015). Variation chosen in this study was selected to mimic evolutionary shifts in bone shape that could affect glenohumeral biomechanics. As an initial study, the present results could be used to guide future analyses. Based on the present results, more generous standard deviations could be applied to test the broader effect of specific physical feature inputs on musculoskeletal output function. Changes made to some geometric features may require concurrent changes not addressed here to have the hypothesized effect. Physical features such as the origins of the rotator cuff may have a larger effect with concurrent variation of the insertion of the rotator cuff on the humeral head (Larson & Stern, 1992). Glenoid inclination may require simultaneous perturbations to the scapular spine and acromion angle (Larson & Stern, 2013). Based on the present results, physical features being perturbed in isolation of highly correlated physical features will not have the hypothesized effect on function.

Monte Carlo analyses output sensitivity factors that must be interpreted with some caution. First, unlike with AMV, sensitivity factors produced by Monte Carlo are not present in normalized space that allows cross-comparison of each of the inputs, but as the effect of shifting an input factor by its single standard deviation unit on the output distribution. However, while magnitudes can only be qualitatively compared across numerous inputs of different variability, the most significant inputs for all outputs were those with the smallest standard deviation unit (muscle insertions). Second, while sensitivity of the output distributions is demonstrated in the factors, the actual directional effect of each input on the output is unknown. It may be worthwhile in future work to assess the sensitivity of output values by performing isolated, standardized perturbations in each of the inputs to determine the magnitude of the effect of each input. Finally, due to averaging, there is a loss of resolution of the sensitivity factors with respect to probability levels and climbing static instances. Sensitivity values were averaged to improve interpretability of the results. Averaging sensitivity factors is a common procedure, especially in gait analysis (Laz & Browne, 2010). Close inspection of the sensitivity factors determined limited changes to sensitivity factors across probability levels and climbing static instances.

6.8 Conclusion

Computational and probabilistic modeling is increasingly used in a variety of scientific fields, but is still very novel in evolutionary science. There are plentiful benefits to introducing computational modeling to answer evolutionary questions about human function. Numerous limitations have been identified with traditional methods of analysis such as comparative morphometrics, including the method of measurement, and what and how many features to compare (Green et al., 2016; Larson & Stern, 2013; Smith, 2016; Young et al., 2015). Computational modeling can build upon previous comparative work by integrating the entire musculoskeletal system into an evolutionary and biomechanical analysis of human function in a variety of scenarios (Hutchinson, 2012; O'Neill et al., 2014). Incorporating probabilistic methods increases the faculty of computational models to evaluate the effect of specific physical features on population level function (Laz & Browne, 2010).

Comparing modern humans to related extant and extinct species is important to study of human evolution, as well as clinical and biomechanical study of modern human function. The capabilities of the modern human shoulder are not fully understood, including the root cause of common injuries and disorders. Limitations of the human shoulder are rooted in evolutionary adaptations to the region. The human upper extremity has evolved essential strengths, such as high-velocity throwing and fine motor control (Cartmill & Smith, 2009; Roach et al., 2013; Wood & Richmond, 2001). However, consequential vestigial adaptations have occurred alongside these beneficial adaptations. Understanding why these less ideal adaptations have occurred is essential to combating and treating the resulting modern human joint disorders.

This study aimed to assess the form-function relationship through variation of evolutionarily relevant physical features of the glenohumeral joint. The results reinforced the differences between human and chimpanzee rotator cuff function. Humans remained reliant on the infraspinatus and teres minor and were predicted to overload both muscles in the support phase of the climbing cycle. Chimpanzees had more dispersed muscle forces across all rotator cuff muscles for the climbing cycle support phase.

The results give insight into the evolutionary foundation of rotator cuff injuries in modern humans. The human rotator cuff muscles have become smaller to accommodate the evolutionary shift to a non-weight-bearing usage of the upper extremity. These muscles easily become unable to provide synergistic activity to counter the action of the large and strong deltoid muscles in overhead postures, leading to early onset muscle fatigue. This leads to imbalances of muscle forces about the glenohumeral joint. While these evolutionary changes are beneficial to many modern upper extremity behaviors such as carrying, tool manipulation, and throwing, they also lead to pathological changes to the biomechanics of the joint in high force behaviors that initiate injury pathways.

The complexity of the form-function relationship has also been highlighted by this work. Sensitivity factors indicated that muscle attachment positions have the greatest effect on muscle force distributions. Yet, this was not a direct relationship, as perturbation of each muscle attachment position affected numerous output muscle distributions. While physical form clearly affects function, the interdependency of the glenohumeral joint makes it difficult to isolate specific features as limiting a specific ability. The strengths and weaknesses of modern human shoulder function, and its capacity for evolutionarily relevant behaviors, are reflective of the evolutionary adaptation of numerous physical features. The species-specific variability of all musculoskeletal features biomechanically interact to support joint function.

Chapter 7 Contributions

The prosperity of the human species is unparalleled in the natural world. Humans have migrated and travelled to all corners of the globe, and for better or worse, humans have touched and changed nearly all life on earth. Despite such impact, humans have only left evidence of activity during a mere fraction of the earth's life. In this time, humans have evolved and adapted from primates scavenging for food amidst the African tree canopies, to the complex and diverse, but wildly connected bipedal beings that span the globe. The highly developed modern human mind has sought to understand how such development came to be over such a short time period.

Born out of human curiosity, fields such as anthropology have pursued answers to questions about the history of human development, including diverse concepts of culture, society, and physical origins and progressions. Anthropological endeavors have provided substantial initial insights into these linked topics. But to further the understanding of human evolution, integration with other fields of study is necessary to address previously unanswered questions.

Anthropological research methods have attempted to close the gaps in the understanding of human evolution, though many questions still remain unanswered. Humans may have evolved from an arboreal common ancestor with chimpanzees, to become modern committed bipeds. How the requisite physical adaptations toward bipedalism were achieved and what this has meant for modern human function, including injury risk, is unknown. Physical anthropology has traditionally employed an approach of making select morphological comparisons between and within species to infer how physical adaptations changed functional capacity and locomotor and non-locomotor choices in humans. Morphometric comparative methods have amassed an abundance of knowledge regarding human evolution and function. However, introducing biomechanical modeling has the potential to integrate the complexity of the entire musculoskeletal system into evolutionary analyses, allowing observation of how physical adaptations affect many functional outcomes.

As a first step in comparative evolutionary biomechanics, the chimpanzee shoulder represents a musculoskeletal system with overall similarity to humans, but with important distinctions. The musculoskeletal structure of the chimpanzee shoulder is very similar to humans (Young, 2008). There is also a large functional overlap between the two species. However, the primary function of each species has diverged since the split from a common ancestor. The human shoulder has become highly proficient at non-locomotor behaviors while the modern chimpanzee shoulder retains possible ancestral arboreal proficiency. This divergence of primary function has led to important structural differences between the closely related species. These specific musculoskeletal differences could explain the human evolution of rotator cuff pathology concurrently with the devolution of the arborealism in favor of the non-locomotor

7.1 Summary of Research

This work integrated biomechanical experimental, musculoskeletal modeling and probabilistic modeling methods with anthropological paradigms to study the effect of morphology on the overhead locomotion capacity of the non-locomotor human shoulder and locomotor chimpanzee shoulder. The ultimate outcome was a probabilistic comparison between an existing human musculoskeletal glenohumeral model and a novel chimpanzee musculoskeletal glenohumeral model that assessed the effects of anthropologically notable upper extremity morphological variation.

7.1.1 Experimental Research

Experimental analysis of human horizontal bimanual arm-suspension climbing demonstrated the difficulty of performing ancestral, weight-bearing upper extremity locomotor tasks in modern humans. Though highly variable, all human participants had high muscle forces and large ranges of overhead postures. Experienced climbers completed the climbing task using moderately reduced muscle activity compared to inexperienced climbers. These group differences demonstrated that moderate training adaptations are possible to improve climbing ability in modern humans. Compared to previously published chimpanzee data, humans recruited the shoulder musculature at a much higher percentage of maximal capacity. Similar muscle activity patterns were found between humans and chimpanzees, linking shoulder function of two closely related species. However, notable differences existed, even between the experienced climbers and chimpanzees, particularly in the deltoid muscles. The posterior deltoid muscle was not used as a powerful propulsive muscle in modern humans, as it is in chimpanzees. This is likely associated with divergent modern usage of the upper extremity. Chimpanzees habitually use their powerful deltoid muscles in high force, high velocity locomotor behaviors. The human deltoids, though still relatively strong, have evolved to accommodate modern upper extremity behaviors of lower force. The kinematic and muscular similarities indicate strong functional musculoskeletal connection between the two species in climbing strategies, and possible evidence to support brachiating past for the human lineage.

7.1.2 Computational Modeling

The deterministic chimpanzee glenohumeral model and between species anthropological probabilistic methods that were employed were the first of their kind. The deterministic model predicted notable differences between chimpanzees and humans in glenohumeral muscle forces. The chimpanzee model predicted much lower muscle forces than humans to stabilize and prevent traction at the glenohumeral joint. The human model limited rotator cuff muscle activity to the infraspinatus and teres minor only, whereas the chimpanzee model engaged all rotator cuff muscles at lower force levels in all these muscles. These results implicated the evolutionary adaptations to the rotator cuff in humans that has limited full contribution of the muscle group to weight-bearing and locomotor tasks.

The probabilistic simulations broadened the deterministic analysis by considering the effect of musculoskeletal variability on rotator cuff muscle function. Numerous musculoskeletal traits have been implicated as evolutionarily significant, and associated with functional adaptations of the shoulder. The probabilistic simulation reinforced the results of the deterministic analysis. Perturbing rotator cuff origins, deltoid insertion, glenoid inclination and intrinsic joint stability did not cause rotator cuff muscle force convergence between chimpanzees and humans. However muscle insertions and origins had the greatest effect on the predicted muscle force distributions. The human glenohumeral model remained infraspinatus and teres minor dominant. The predicted confidence intervals for human infraspinatus and teres minor suggest bimanual climbing will overload both these muscles.

Though species gross musculoskeletal geometry is similar, differences between the two species models were rooted in different base joint orientation and muscle architecture. Specifically, the human glenohumeral joint is laterally orientated, shoulder muscle absolute and relative physiological cross sectional area (PCSA) is reduced, and the inter-muscular relative force producing relationship is adapted away from high force, weight-bearing. While all human shoulder muscles are reduced in absolute PCSA relative to chimpanzees, the human rotator cuff muscles have reduced even more relative to the deltoids. These muscles are less capable of offsetting the strong superior force of the deltoid muscles in overhead and weight-bearing postures. The human glenohumeral joint has become highly reliant on infraspinatus to counter the activity of the deltoids, which superiorly translates the humeral head. This problem is compounded by the laterally orientated human glenohumeral joint that has reduced subacromial space due to the more laterally projected acromion. While this musculoskeletal geometry has improved human glenohumeral function below shoulder height, it has complicated function in overhead and evolutionarily relevant postures.

7.2 Implications for Evolutionary Science

This work exemplified the utility of biomechanical modeling in the field of anthropology. The present glenohumeral models expanded the foundation of anthropological undertakings in upper extremity evolution beyond contemporary comparative techniques. With a human and chimpanzee model, representing both a non-locomotor upper extremity, and an arboreal and terrestrial locomotor upper extremity, respectively, more musculoskeletal biomechanical models can be produced of other close primate relatives and fossilized remains of ancient humans. Future comparisons of modern human, primate and ancient human models could broaden perspectives on the relationships between musculoskeletal form and function across a wider spectrum of species, and the evolutionary adaptations that may relate to the host of human locomotor adaptations from brachiation to bipedal. Through these analyses, a new depth of knowledge may be obtained about the unique evolutionary experience of humanity and human connectivity to the rest of the animal kingdom.

This research provided some evidence for a human brachiating past. There were large commonalities between species in climbing strategies – both kinematics and muscle activity – in experimental scenarios. The computational musculoskeletal models further the general common muscular activity between chimpanzees and humans. Where the two species differed most notably was musculoskeletal geometry and force sharing about the deltoids and rotator cuff muscles. Modern divergence of humans from chimpanzee-like arborealism follows a conceivable path from a superiorly oriented and more massive shoulder musculature to the laterally oriented, less massive modern human musculoskeletal form. The specific divergence observed in the human muscular strategies has a strong likelihood of being derived through devolution of brachiation in humans. However, without similar research into other hypothesized ancestral locomotor means, such as quadrupedal terrestrial walking, this evidence is incomplete.

The probabilistic analysis was limited in scope, but demonstrated the complexity of the form and function relationship. Morphological traits can be associated with specific species, taxa, physical behaviors and locomotion. However, based on the present results, caution should be used when attempting to isolate specific boney features as being indicative of the hominin musculoskeletal phenotype. Isolated features may not modulate function substantially without concurrent, related physical changes. Also, the effect of specific features on function, particularly specific muscle positions, is diffused, affecting physical capacity in numerous ways. Subsequently, the relationship between morphological traits and functional capacity needs to be carefully considered. Continuing research on form and function should take into account what traits are correlated, and what traits should be considered in combination.

7.3 Implications for Human Function

Through experimental and computational modeling, climbing was shown to be a strenuous task in modern humans and highly variable, but grossly similar to chimpanzee climbing techniques. The human shoulder musculature was highly recruited, especially during the support phase of climbing, to counter the effects of gravitational loads and traction at the shoulder. Experienced climbers were more likely to lower muscle activity overall and in transitions between climbing phases. This practice-based adaption is beneficial to the endurance of the task, and also more closely mimics primate behaviors. Muscle recruitment differences between humans and chimpanzees showcased the loss of weight-bearing actions in the human upper extremity. Muscles that were highly active in humans were recruited at much lower levels in chimpanzees, likely due to humans requiring more reserve strength to complete the task. Despite improved musculoskeletal performance in experienced climbers, humans remain highly susceptible to injury during climbing activities. The results of this research demonstrate a need to further study climbing biomechanics and injury mechanisms, the close musculoskeletal relationship between humans and chimpanzees, and the utility of performing comparative experimental, biomechanical analyses.

While the bimanual climbing task is not a typical modern human behavior, it does offer an end-range illustration of the musculoskeletal injury risk posed by overhead exposures. Increased arm elevation requires increased activity from the shoulder musculature (Sood et al., 2007). As the modern human shoulder musculature is relatively small with low force producing capacity, low-force, elevated postures in occupational settings have been observed to cause muscle fatigue and eventual shoulder pain (Anton et al., 2001; Ebaugh et al., 2006; Nussbaum et al., 2001; Sood et al., 2007). Due to the high hand forces, the bimanual climbing task is an overhead task with much greater exposure than those typically seen in occupational settings. In using an evolutionarily relevant, though atypical task, the present analyses explored the biomechanical outcome of a more extreme version of the shoulder exposures typically seen in the workplace. The results of the experimental, computational and probabilistic analyses demonstrate shoulder muscle activity that would rapidly lead to fatigue, and potentially compensatory and problematic biomechanics. Further, less efficient muscle mechanics in overhead postures compound this risk by compromising the contribution of important human shoulder muscles, such as the supraspinatus and subscapularis, to glenohumeral joint stability. The results agree with and further previous occupational biomechanical research. High-force, overhead postures require shoulder biomechanics that are associated with muscle fatigue, synergist imbalance and increased injury risk. The evolutionary analysis provided primary research for explaining the roots of occupational and recreational shoulder pathology.

Evolutionary roots of injury mechanisms were highlighted in the overall results of the present thesis. The propensity for rotator cuff disorders in modern humans is likely a vestigial adaptation borne out of upper extremity adaptations paralleled with the evolution of habitual bipedalism. As humans became habitually bipedal, the upper extremity became devolved for locomotor purposes, and increasingly adapted for important non-locomotor behaviors. This shifted the muscle force-sharing relationship and geometry of the glenohumeral joint toward upper extremity behaviors in a range of motion below shoulder, lateral and anterior to the body. The current geometry of the human upper extremity has evolved for high utility in non-weight-bearing behaviors, and this specific shoulder evolution may be linked to the extraordinary development and prosperity of the human species. However, the comparative analyses of the present results demonstrate that these adaptations have consequences for secondary upper extremity behaviors. Owing to the large range of motion of the shoulder, humans are still capable of weight-bearing and overhead behaviors. However, this inclusive human capacity is limited by evolutionary adaptations.

Finally, the present experimental and probabilistic analyses furthered research into population-level musculoskeletal variability. The human population is highly variable, and capable of very different shoulder biomechanics to complete the same climbing task. In particular, muscular recruitment can be highly divergent. Probabilistic analyses that perturbed musculoskeletal features provided insight into how some morphological features can affect joint function. However, human variability and muscle force distributions never converged with the performance of the habitually brachiating chimpanzee species. Despite similarities with chimpanzees, and a likely arboreal past, modern humans are unlikely to present with a morphology that could lessen overhead and weight-bearing fatigue-related injuries at the shoulder, similar to that of the chimpanzee species. However, within species variability in specific musculoskeletal features likely modulates individual injury risk. As research continues into the effects of population level variability, more expansive probabilistic analyses will provide insight into what combinations of morphological features affect specific musculoskeletal capabilities. Chimpanzees provide a strong, human-linked musculoskeletal framework to study a less injury prone shoulder complex. Continuing comparative probabilistic analyses between species will not only improve interpretations of evolutionary adaptations of the human shoulder, but also estimations of human functional capacity and injury risk.

7.4 Future Directions

There is limited comprehensive research on human climbing biomechanics. This is concerning due to the large range of upper extremity musculoskeletal injuries experienced by climbers. The narrow climbing technique explored in the present research was chosen to replicate extant chimpanzee studies of climbing. Future experimental studies should be expanded to other forms of recreational and competitive climbing, including wall and rock climbing, vertical climbing, and bouldering. Studies should include anthropometric, sex and morphological considerations that may affect climbing abilities, strategies and propensity for injury. Shoulder rhythm should also be captured in climbing experimentation, as there may be quantifiable differences in the scapular rhythm of competitive climbers from other populations.

The use of the chimpanzee model can be broadened beyond the objectives of the present work. The chimpanzee model was designed to be easily modified should other research questions arise or new data become available. The model can expand to include the entire shoulder complex, including the acromioclavicular and sternoclavicular joints and the musculature modulating motion at these joints. The model accepts any kinematic inputs. With simple modifications to hand force measures, the model can analyze a wide range of upper extremity tasks, including evolutionarily relevant tasks such as quadrupedal climbing, vertical climbing and quadrupedal terrestrial locomotion and human-centric tasks such as reaching, carrying, and throwing. Very little data currently exists on chimpanzee musculoskeletal biomechanics, including three-dimensional kinematics, shoulder rhythm and tissue mechanics and architecture. The model can accept novel chimpanzee musculoskeletal data as it becomes available. Alternatively, the benefit of computational models is they can be used to simulate scenarios that are difficult or infeasible to perform experimentally. The geometry module can be modified to represent and answer deterministic musculoskeletal hypotheses, such as removing a muscle, enlarging the absolute PCSA of specific muscles, or altering the shoulder rhythm.

Finally, probabilistic modeling should be expanded upon with subsequent analyses of additional physical traits and functional outputs. However, this approach should be carefully measured and consider previous anthropological work. New physical input features and functional output features to be analyzed probabilistically should use comparative morphometric analyses as a guide. A next logical step would be to perform a probabilistic simulation that concurrently perturbs the angle of scapular spine and acromion, height of the glenoid, and inclination of the glenoid on muscle forces about the glenohumeral joint. Further, outputs should be expanded to include the deltoid muscles.

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Appendix A

The all-subsets regression model approach selected the combination of variables that created the best fit model for each of the three chimpanzee scapula and clavicle equations, referred to as *Chimp2* (Equations 16-21). Any variable that contributed less than 2% to the explanation of the model was removed (Grewal, 2012).

Equation 16: Best-fit equations predicting the chimpanzee scapular rotation of retraction/protraction (γ). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\gamma_{S\_Chimp2} = -120.5 + (0.686\ \gamma_{TH0}) + (-3.383\ \beta_{TH}) + (0.02098\ \beta_{TH}^{2}) + (0.0133\ \gamma_{TH0}\ \beta_{TH})$$

Equation 17: Best-fit equations predicting the chimpanzee scapular rotation of lateral/medial rotation (β). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\beta_{S\_Chimp2} = 54.2 + (1.026\ \beta_{TH}) + (0.00475\ \beta_{TH}^{2}) + (-0.0048\ \gamma_{TH0}\ \beta_{TH}) + (0.00239\ \beta_{TH}\ \gamma_{TH1})$$

Equation 18: Best-fit equations predicting the chimpanzee scapular rotation of anterior/posterior tilt (α). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\alpha_{S\_Chimp2} = 96.6 + (-0.1632\ \gamma_{TH0}) + (1.929\ \beta_{TH}) + (0.0724\ \gamma_{TH1}) + (0.01224\ \beta_{TH}^{2}) + (-0.0012\ \gamma_{TH0}\ \beta_{TH})$$

Equation 19: Three original, best-fit equations predicting the chimpanzee clavicular rotation of elevation/depression (β). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\gamma_{C\_Chimp2} = 32.1 + (0.285\ \gamma_{TH0}) + (0.642\ \beta_{TH}) + (0.1584\ \gamma_{TH1}) + (-0.00973\ \gamma_{TH0}\ \beta_{TH})$$

Equation 20: Three original, best-fit equations predicting the chimpanzee clavicular rotation of retraction/protraction (γ). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\beta_{C\_Chimp2} = 20.3 + (-0.1494\ \gamma_{TH0}) + (1.826\ \beta_{TH}) + (-0.0835\ \gamma_{TH1}) + (0.01143\ \beta_{TH}^{2}) + (-0.01081\ \gamma_{TH0}\ \beta_{TH})$$

Equation 21: Three original, best-fit equations predicting the chimpanzee clavicular rotation of forward/backward rotation (α). The three thoracohumeral rotations used to predict the scapular and clavicular rotations are represented as plane of elevation (γ_{TH0}), elevation (β_{TH}), and internal/external rotation (γ_{TH1}).

$$\alpha_{C\_Chimp2} = 55.3 + (0.122\,\gamma_{TH0}) + (0.086\,\beta_{TH}) + (0.1312\,\gamma_{TH1}) + (0.00918\,\gamma_{TH0}\,\beta_{TH})$$

The fit of the ‘all subsets’ *Chimp2* equations and the *Chimp* equations was compared through r-squared and RMS error values (Table 15). Morphological realism was assessed through comparison of the intercept values (Table 16). The *Chimp2* equations had higher r-squared values and smaller RMS error, demonstrating an equation with a stronger fit than *Chimp* equations. The *Chimp2* equations predicted high, anatomically unrealistic intercept values across all equations (Table 16).

Table 15: The regression analysis outputs of r-squared and RMS error showing the strength of fit of both sets of equations describing the chimpanzee shoulder rhythm.

		γ_S	β_S	α_S	γ_C	β_C	α_C
Chimp	R-squared	0.47	0.75	0.42	0.57	0.70	0.31
	RMS Error	8.37	4.03	3.96	10.29	3.94	14.1
Chimp2	R-squared	0.76	0.82	0.77	0.79	0.88	0.36
	RMS Error	5.84	3.45	2.64	7.6	2.65	13.53

Table 16: A comparison of the intercept values for the two sets of chimpanzee equations and the human equations. These values give a sense of the anatomical realism of the baseline predictions of all the equations. The human data is included to provide a comparative value.

		γ_S	β_S	α_S	γ_C	β_C	α_C
Intercept	***Chimp***	-3.91	20.28	31.83	-4.2	-40.52	67.0
	Chimp2	-120.5	54.2	96.6	32.1	20.3	55.3
	Human	30.1	-1.68	-11.2	-13.3	-14.6	0.411

Due to the limited data set of chimpanzee joint angles, the ‘all-subsets’ method produced higher order functions and a stronger fit, but with anatomically unrealistic intercept values. A stronger fit regression analysis can usually be obtained through inclusion of higher order variables, such as quadratic and cubic functions (Miller, 2006). However, in small sample sizes, there is greater risk of outlier values having greater weight in the overall prediction than is reasonable to their probabilistic likelihood (Miller, 2006). Due to the small data set in the present study, the better fit of *Chimp2* does not mean it is a better representation of true chimpanzee shoulder rhythm. Previously derived human regression equations have typically determined most scapular and clavicular rotations to be linear (de Groot & Bland, 2001; Grewal & Dickerson, 2013; Makhsous, 1999; Xu Xu et al., 2014). Chimpanzees are considered to have a relatively similar upper extremity structure to humans, and have had their scapular orientation grouped with humans (Inman et al., 1944; Lewis et al., 2001; Schmidt & Krauss, 2011). It stands to reason that the shoulder rhythm should be similar in its composition and trajectory to humans as well. As the *Chimp2* equations were considered anatomically unrealistic, they were not considered to be a representative estimation of the chimpanzee shoulder rhythm.

Glossary

Term	**Definition**
Climbing	General term describing any activity using the hands, feet or other body part to ascend a steep object. Inclusive of vertical and horizontal tree climbing, rock and wall climbing, bouldering.
Arboreal	A generic term describing primate locomotor behaviors in trees. Inclusive of vertical and horizontal climbing, as well as hanging and suspensory behaviors.
Brachiation	Arm swinging. A type of arboreal locomotion using only the upper extremity to swing from supports.
Bimanual Climbing/Horizontal bimanual arm suspension climbing	Refers specifically to the task examined in the present study. A simulated horizontal climbing task performed across a set of equally spaced rungs.